THE SYNERGISTIC EFFECTS OF ENVIRONMENTAL CHANGE ON THE POPULATION DYNAMICS OF LOCALIZED ENDEMIC SPECIES, A CASE STUDY IN HAWAIʻI

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Abstract

The spatial distribution and abundance of organisms are shaped by interactions with the environment. Human-induced changes in the environment can have varying effects on plant vital rates across ontogeny, sometimes in opposite directions. It is commonly thought that plant endangerment is the result of the combined effects of multiple environmental stressors. The influences of environmental stressors on components of plant fitness have been well examined. Few studies, however, have explicitly evaluated the synergistic effects of environmental stressors on the geospatial distribution of endangered species. In this dissertation I examined the population dynamics of three Hawaii endangered plants, *Schiedea obovata, Cyrtandra dentata,* and *Delissea waianaeensis*. Furthermore, I used a combination of size and stage structured demographic models to quantify the individual and combined impacts of dominant non-native pests and changing abiotic conditions on plant dynamics. I also compared the economic costs of various restoration strategies, including the suppression of non-native frugivores and seedling herbivores. I found that for *S. obovata and C. dentata,* fine-scale changes in microhabitat heterogeneity and inter-annual precipitation patterns had a greater effect on plant dynamics than top-down stressors. Furthermore, I found that the endangered plant populations were not always at, or close to, their equilibrium state (i.e., stable stage distribution SSD). There are many factors that contributed to the populations moving away from equilibrium, including population augmentation and the suppression of non-native pests. For the *D. waianaeensis and C. dentata* populations, there was a greater proportion of individuals in later life stages than would be expected if the populations were at a stable equilibrium. High reproductive value of these populations

caused them to grow faster in the near-term transient phase (i.e., 10 years) than over the long-term as the population reached equilibrium (i.e., transient amplification). Furthermore, I found that there were numerous combinations of restoration actions that would likely shift the growth rate of endangered species from declining to growing. However, the yearly economic costs of targeted restoration actions were highly variable. From a global perspective, this study illustrates that changing precipitation patterns and alterations in microhabitat can have a greater negative impact on plant dynamics than non-native frugivores and seedling herbivores and thus should be considered when developing rare plant restoration strategies. This research also emphasizes how important it is to evaluate both the near term transient and asymptotic dynamics of endangered species in order to fully capture the likely outcome of restoration effort

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Chapter 1 Introduction

The spatial and temporal distribution and abundance of organisms are shaped by interactions with the environment. Human-induced changes in the environment, such as alterations in plant-animal interactions and degradation in abiotic conditions, influence demographic vital rates (i.e., survival, growth, and reproduction) and population dynamics. Recent research suggests that plant endangerment is the result of the combined influence of multiple environmental stressors (Brook et al., 2008, Sala et al., 2000, Didham et al., 2007). To explicitly evaluate the individual or combined influence of environmental change on population growth rate requires a demographic modeling approach (Morris and Doak, 2002). Though many demographic studies have quantified the influence of various environmental factors on plant population dynamics, few studies have focused on the synergistic effects of non-native species and changing environmental conditions, such as spatial and temporal alterations in precipitation and temperature (Souther and McGraw, 2014, Dávalos et al., 2014, Brook et al., 2008).

One of the most widely used restoration strategies to prevent species extinction is to suppress top-down competitors and predators (i.e., environmental stressors) (Soorae, 2011, Maschinski and Haskins, 2012). There is clear evidence that the effect of environmental stressors can have differing effects on plant vital rates across ontogeny (Maron and Crone, 2006). The effect of environmental stressors on population dynamics can also vary along an ecological gradient and be context specific (Miller et al., 2009, Dahlgren and Ehrlén, 2009, Gaoue et al., 2011, Gaoue and Ticktin, 2010). There is also a

small, but growing, body of literature that suggests the key demographic processes that drive population dynamics in the long-term can be a poor predictor of the relative importance of key life stages on population dynamics in the near term (Gaoue, 2016, Haridas and Gerber, 2010, Haridas and Tuljapurkar, 2007, McMahon and Metcalf, 2008, Ezard et al., 2010a). With a limited number of studies that have compared the relative difference between near term transient dynamics (10 year projections) and long-term asymptotic dynamics, however, it is impossible to determine what demographic processes, such as life form or generation time, can be used to determine if and under what circumstances long-term projections are an accurate proxy of transient dynamics. Identifying under what circumstances long-term dynamics do not accurately represent near term transient dynamics is particularly important for prioritizing restoration strategies for rare species on the brink of extinction.

With an increase in the listing of rare and at-risk species (IUCN, 2013) and continual anthropogenic change in environmental conditions, the reintroduction of endangered species has also become one of the most widely used restoration strategies for species that have reached critical low population density (Maschinski and Haskins, 2012). The end goal of this restoration strategy is to prevent imminent extinction and promote the recovery of species over time (Maschinski and Haskins, 2012). Many studies have synthesized what aspects to consider when planning the reintroduction of endangered species, such as identifying what type of propagule (e.g., seeds or reproductively mature plants) should be used to establish populations in order to achieve the highest rate of survival and short-term persistence (Maschinski and Haskins, 2012).

Conversely, the long-term outcome of reintroduced populations is rarely examined (Menges, 2008). A recent study, however, suggests the long-term persistence of reintroduced populations is alarmingly low; with six out of eight reintroduced species disappearing after 15 years (Drayton and Primack, 2012). "*Given the nature of human motivation to accentuate success and minimize failures* (Menges, 2008)," the long-term outcome of reintroduction populations are likely bias towards success. The low rate of long-term persistence of reintroduced populations is due, in part, to the widespread disturbance of ecosystems in which rare species occur (climate change and invasive predators, competitors, and pathogens). In these altered landscapes, it is critically important to identify which environmental stressors need to be suppressed following the reintroduction of species in order to achieve the desired outcome (i.e., population growth rate $\lambda \geq 1$). The suppression of top-down environmental stressors and the reintroduction of endangered species are time intensive and costly and thus, it is critically important to develop biologically and economically efficient restoration strategies.

Tropical islands are biodiversity hotspots and, unfortunately, have some of the highest rates of extinction and species endangerment. For these reasons, tropical island ecosystems are often ranked as high conservation priority (Myers et al., 2000, Mittermeier et al., 1998). The high rates of extinction and species endangerment on islands are due, in part, to the sheer number of localized endemic species (Menges, 1990, Gilpin and Soule, 1986, Shaffer, 1981, Brigham and Schwartz, 2003). Due to their geographically limited range and adaptation to narrow ecological conditions (Brown, 1984), island endemic plants are more sensitive to environmental change than common

widespread species. Consequently, even small-scale changes in the environment may have a disproportionally large effect on the population persistence of island plants. Thus, to effectively manage endangered species in an island context, it is critical to understand how fine-scale alterations in the environmental influence population persistence (Myers et al., 2000, Mittermeier et al., 1998). Surprisingly, the demographic consequence of plant interactions with environmental stressors is rarely studied for localized island endemic species (but see, Krushelnycky et al., 2013, Simmons et al., 2012).

In this study, I used a combination of size and stage based demographic models to examine the population ecology of three localized endemic oceanic island species native to Hawai‘i. Additionally, I evaluated the synergistic effects of changing abiotic conditions and the introduction of top-down stressors on the population dynamics of endangered species. For this study, I also used demographic models to develop ecologically and economically effective restoration strategies for localized endemic plants confined to narrow ecological conditions. The species selected for this case study were three endangered taxa native to Hawai‘i, *Cyrtandra dentata* St. John & Storey (Gesneriaceae), *Delissea waianaeensis* Lammers (Campanulaceae) and *Schiedea obovata* (Sherff) W.L. Wagner & Weller (Caryophyllaceae). The *D. waianaeensis* and *S. obovata* sites were reintroduced populations and *C. dentata* site was a naturally occurring population. Specifically, the research objectives that I addressed in this dissertation were:

1. Evaluate the impact of microhabitat heterogeneity and a non-native avian frugivore on the near term transient and long-term asymptotic dynamics of *Cyrtandra dentata*.
2. Assess the individual and combined effect of inter-annual precipitation and non-native seedling herbivores on the population dynamics of *Schiedea obovata*.
3. Examine the near-term transient and long-term asymptotic dynamics of species reintroductions.
4. Evaluated the effect of biologically meaningful increases (i.e., perturbations) in survival, growth, and fertility on the dynamics of endangered species and identify which combination of restoration efforts are the most economically efficient.

These four research objectives are outlined in detail in Chapters 2–5, respectively. To conclude my dissertation, in Chapter 6 I summarize my key research findings and outline how this research contributions to the fields of population ecology and conservation biology. In Chapter 6 I also discuss the conservation implications of my research and propose future research that is needed to understand the population ecology of oceanic islands species and accurately predict how environmental change will impact the spatial and temporal dynamics of endangered species.

Declaration

Chapters 2-5 of this dissertation are based on manuscripts that are either published or in review, which were jointly authored and have been edited to comply with the format of this dissertation.

Chapter 2: Bialic-Murphy, L., Gaoue, O., and Kawelo K. (2017). Microhabitat heterogeneity and a non-native avian frugivore drive the population dynamics of an island endemic shrub, *Cyrtandra dentata*. Journal of Applied Ecology, *in press*.

Chapter 3: Bialic-Murphy, L. and Gaoue, O. Low inter-annual precipitation has a greater negative effect than seedling herbivory on the population dynamics of a short-lived herb, *Schiedea obovata* (Caryophyllaceae). Ecology and Evolution, *in revision.*

Chapter 4: Bialic-Murphy, L., Gaoue, O., and Knight, T. Evaluating both the transient and asymptotic dynamics is critical for assessing the efficacy of species reintroductions. Conservation Biology, *in review.*

Chapter 5: Bialic-Murphy, L., Gaoue, O., and Knight, T. Developing economically efficient restoration strategies for critically endangered plants, a case study in Hawaii. Ecological Applications, *in advanced preparation.*

Chapter 2 Microhabitat heterogeneity and a non-native avian frugivore drive the population dynamics of an island endemic shrub, *Cyrtandra dentata*

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Running title: Population dynamics of an endemic plant

Keywords: Cyrtandra dentata, stage-structured demographic model, stochastic demography, transient dynamics, endangered species, plant population dynamics, restoration ecology, elasticity analysis, avian frugivory, microhabitat heterogeneity

Abstract

1: Understanding the role of environmental change in the decline of endangered species is critical for designing scale-appropriate restoration plans. For locally endemic rare plants on the brink of extinction, frugivory can drastically reduce local recruitment by dispersing seeds away from geographically isolated populations. Dispersal of seeds away from isolated populations can ultimately lead to population decline. For localized endemic plants, fine-scale changes in microhabitat can further limit population persistence. Evaluating the individual and combined impact of frugivores and microhabitat heterogeneity on the short-term (i.e. transient) and long-term (i.e. asymptotic) dynamics of plants will provide insight into the drivers of species rarity.

2: In this study, we used 4 years of demographic data to develop matrix projection models for a long-lived shrub, *Cyrtandra dentata* (H. St. John & Storey) (Gesneriaceae), which is endemic to the island of O'ahu in Hawai'i. Furthermore, we evaluated the individual and combined influence of a non-native frugivorous bird, *Leiothrix lutea*, and microhabitat heterogeneity on the short-term and long-term *C. dentata* population dynamics.

3: Frugivory by *L. lutea* decreased the short-term and long-term population growth rates. However, under the current level of frugivory at the field site the *C. dentata* population was projected to persist over time. Conversely, the removal of optimum microhabitat for seedling establishment (i.e. rocky gulch walls and boulders in the gulch bottom) reduced the short- term and long-term population growth rates from growing to declining.

4: Survival of mature *C. dentata* plants had the greatest influence on long-term population dynamics, followed by the growth of seedlings and immature plants. The importance of mature plant survival was even greater when we simulated the combined effect of frugivory and the loss of optimal microhabitat, relative to population dynamics based on field conditions. In the short-term (10 years), however, earlier life stages had the greatest influence on population growth rate.

5: Synthesis and applications. This study emphasizes how important it is to decouple rare plant management strategies in the short vs. long-term in order to prioritize restoration actions, particularly when faced with multiple stressors not all of which can be feasibly managed. From an applied conservation perspective, our findings also illustrate that the life stage that, if improved by management, would have the greatest influence on population dynamics is dependent on the timeframe of interest and initial conditions of the population.

Introduction

The spatial distribution and abundance of organisms are shaped by interactions with the environment. Human-induced changes in the environment, such as alterations in plant-animal interactions and degradation in abiotic conditions, influence demographic vital rates (i.e., survival, growth, and reproduction) and population dynamics, such as the population growth rate. Recent research suggests that plant endangerment is the result of the combined influence of multiple environmental stressors (Brook et al., 2008, Sala et al., 2000, Didham et al., 2007). To explicitly evaluate the individual or combined influence of targeted environmental change on population growth rate requires a demographic modelling approach (Morris and Doak, 2002). Though many demographic studies have quantified the influence of various environmental factors on plant population dynamics, few studies have focused on the individual or combined impact of non-native frugivores and alterations in abiotic conditions (Godínez-Alvarez and Jordano, 2007, Loayza and Knight, 2010).

Tropical islands are biodiversity hotspots and, unfortunately, have some of the highest rates of extinction and species endangerment. For these reasons, tropical island ecosystems are often ranked as high conservation priority (Myers et al., 2000, Mittermeier et al., 1998). The high rates of extinction and species endangerment on islands are due, in part, to the sheer number of localized endemic species (Menges, 1990, Gilpin and Soule, 1986, Shaffer, 1981, Brigham and Schwartz, 2003). Due to there geographically limited ranges and adapted to narrow ecological conditions (Brown, 1984), island endemic plants are likely more sensitive to environmental change than

common widespread species. As a consequence, even small-scale changes in the environment may have a disproportionally large effect on the population persistence of island plants. Thus, to effectively manage endangered species in an island context, it is critical to understand how changing environmental conditions influence population persistence (Myers et al., 2000, Mittermeier et al., 1998). Surprisingly, the demographic consequence of plant interactions with environmental stressors is rarely studied for localized island endemic species (but see, Krushelnycky et al., 2013, Simmons et al., 2012).

A primary environmental driver of biodiversity loss on islands is the introduction of non-native plants and animals (Wilcove et al., 1998). Some of the most successful non-native animals to invade island ecosystems are non-native frugivores (Meyer and Butaud, 2009, Shiels et al., 2014). The effectiveness of non-native frugivores to replace the role of native frugivores is dependent on the ecological similarity of the dispersal agents (Schupp et al., 2010). Removal of seeds from a population to microsites that are unfavourable for germination and establishment can lead to localized recruitment depression (Godínez-Alvarez et al., 2002, Loayza and Knight, 2010). In contrast, if seeds are not destroyed following consumption and are dispersed away from the population to suitable habitat for establishment, non-native frugivores could have a positive influence on plant dynamics by decreasing conspecific competition and increasing gene flow between isolated plant populations (Howe, 1986, Bacles et al., 2006, Slatkin, 1985, Schupp et al., 2010). Island species are also threatened by habitat degradation and altered abiotic conditions (Wilcove et al., 1998). Altered abiotic conditions, such as a reduction

of optimal microhabitats, can have a particularly pronounced impact on seedling establishment (Dostálek and Münzbergová, 2013, Eriksson and Ehrlen, 1992, Fetcher et al., 1983). The suitability of microhabitat for seedling establishment can be highly variable among species. Important characteristics of optimal microhabitats for seedling establishment include light availability (Denslow, 1980), substrate characteristics (Dostálek and Münzbergová, 2013), disturbance frequency (Crawley and Nachapong, 1985), and sufficient water availability (Fetcher et al., 1983).

In this study, we investigated the combined effects of abiotic and biotic environmental factors on the dynamics of a localized endemic shrub, *Cyrtandra dentata* (H. St. John & Storey) (Gesneriaceae), confined to a narrow ecological threshold on the Island of O‘ahu in Hawai‘i. The biotic stressor that we examined was a non-native generalist bird, *Leiothrix lutea*, and the abiotic factor that we assessed was alterations in microhabitats that varied in suitability for seedling establishment, optimal microhabitat (rock outcrops, defined as boulders covered by moss in the gulch bottom and the rocky gulch walls) and suboptimal microhabitat (soil). To assess how these environmental factors influence local population dynamics we asked the following questions: (i) Do seed frugivory by *L. lutea* and removal of optimal microhabitat influence the short and long-term population dynamics of *C. dentata*? (ii) Under what combination of these stressors does *C. dentata* maintain positive population growth over the short and long-term? (iii) What life stages and associated vital rates have the greatest influence on population growth rate over the short and long-term? (iv) Do the intensity of these

stressors influence the relative importance of life stages and associated vital rates on the short and long-term population growth rates*?*

Materials and methods

Study species

Cyrtandra dentata is an endangered long-lived shrub endemic to the island of O‘ahu in Hawai‘i. *Cyrtandra dentata* reaches reproductive maturity at 0.8 m (L. Bialic-Murphy, unpublished data) and produces white subumbelliform cymes, 3–9 cm long with white fleshy ovate berries, 1–2.6 cm long (Wagner et al. 1999). The mean age of first reproduction for *C. dentata* is 6 years (L. Bialic-Murphy, unpublished data). The reproductive biology of *C. dentata* is poorly understood, but the white flowers it produces suggest it is moth pollinated (OANRP 2003b). The mean number of *C. dentata* seeds per mature fruit is 1,873 (L. Weisenberger, *unpublished data*) and mean seed size is ca. 0.5 mm long (Wagner et al., 1999). The *C. dentata* fruiting season is between September and November, with peak fruiting in October (L. Bialic-Murphy, *unpublished data*). The long-distance dispersal agents for *Cyrtandra* species in the Pacific is unresolved but columbiform birds have been implicated (Cronk et al., 2005). Previous research also suggests passive transport by water is a short-distance dispersal vector for Hawaiian *Cyrtandra* species (Kiehn, 2001). Adventitious roots are produced from the lower section of the main stems, anchoring plants to soil, rocky gulch walls, and boulders in the gulch bottom (L. Bialic-Murphy, *personal observation)*.

Historically, *Cyrtandra dentata* spanned the northern Wai‘anae Mountains and the leeward side of the northern Ko‘olau Mountains on the island of O‘ahu, 300–610 m in

elevation (Wagner et al. 1999). The typical habitat is shady gulch bottoms of mesic to wet forests. In 1996, *C. dentata* was listed as endangered and by 2010, it was restricted to five geographically isolated locations (USFWS, 2012). Of those populations, only two sites, Kahanahāiki and Pahole to West Makaleha, have > 16 mature plants and are representative of plants in earlier life stages (i.e., immature plants and seedlings).

Leiothrix lutea is one of the most common non-native generalist birds in Hawai‘i. The body mass of males is 21.3 ± 0.28 g and the body mass of females is 21.21 ± 0.24 g (Male et al., 1998). *Leiothrix lutea* gut passage time is unknown but the average gut passage time of avian seed and pulp consumers with similar body size (i.e., 19.9–23.8 g) is 1.73 hours (Herrera, 1984). The diet preference of *Leiothrix lutea* is a mix of insects and small–seeded fruits (Male et al., 1998). *Leiothrix lutea* primarily forage in the understory several meters off the ground, rapidly moving from plant to plant (Male et al., 1998). The home range of *L. lutea* in Hawai‘i is 3.07 ha ± 0.32 for males and 2.68 ha ± 0.27 for females (Male et al., 1998). *Leiothrix lutea* pair formation occurs in March and breeding season is from March to mid August. During the non-breeding season, *L. lutea* are highly nomadic, moving in large flocks (<100 individuals) (Male et al., 1998).

Study site and management history

We studied the demography of *C. dentata* in the Kahanahāiki Management Unit (36 ha), located in the northern Wai‘anae Mountain Range, on the island of O‘ahu (21° 32’ N, -158°12’ W) (Table 2.1). Kahanahāiki is a tropical mesic forest with a mix of native and non-native flora and fauna. The mean monthly rainfall is 53–227 mm (Giambelluca et al. 2013), and the mean daily temperature range is 16–24 °C (Shiels &

Drake 2011). The Kahanahāiki population is one of the two known *C. dentata* locations, with more than 16 mature plants and has individuals in earlier life stages (i.e., seedlings and immature plants). The population is located in the main Kahanahāiki drainage, spanning from the base of a seasonal waterfall to approximately 150 meters to the north. Within the Kahanahāiki drainage, the plants are scatter throughout the gulch bottom and along the steep rock walls. Though plants occur throughout the study site, they are rooted in higher density on rock outcrops than on soil.

Since 1995, the O'ahu Army Natural Resources Program (OANRP) has managed the Kahanahāiki *C. dentata* population. Restoration efforts by OANRP included the control of feral pigs (*Sus scrofa*) and semi-annual suppression of ecosystem-altering invasive vegetation (OANRP, 2009). *Sus scrofa* directly impact many plants through their physical disturbance to the forest. In general, native seedlings, saplings, and mature plants increase in density following *Sus scrofa* control (Busby et al., 2010, Cole et al., 2012, Loh and Tunison, 1999). Non-native plants are a threat through their competitive displacement of native plants (Vitousek, 1996, Ostertag et al., 2009, Minden et al., 2010). Following the suppression of these top-down stressors in the Kahanahāiki fence, *C. dentata* started establishing at higher rates leading to greater numbers of seedlings and small juvenile plants (M. Kiehn, *unpublished data*).

Demography data and projection matrix model

The life cycle of *C. dentata* was divided into four biologically discrete life stages based on height to the apical meristem: reproductive mature (> 80 cm), large immature (20 cm–80 cm), small immature (2 cm–20 cm) plants, and seedling (< 2 cm). We used 80

cm as the cut off for the reproductive mature life stage because it was the minimum height that plants produced fruits at the study site. Small and large juvenile were divided into two categories based on expert opinion by conservation practitioners and observed differences in survival at the field site. In 2010, at the start of this study, the Kahanahāiki *C. dentata* population consisted of 45 mature plants, 158 immature, and 600 seedlings. For four consecutive years (2010–2014), we permanently tagged and monitored a subset of plants in the population annually. Over the study period, a total of 507 plants were tagged and monitored. For the mature and large immature life stages, all individuals were monitored. For the small immature and seedling life stages, we monitored a minimum of 60 plants annually to ensure our effects on *C. dentata* habitat were minimal. For each tagged plant, we collected data on height to apical meristem (when possible), survival, and reproduction.

We used these field data to estimate the survival, growth, and fecundity rates for each life stage and parameterize a matrix projection model (Caswell, 2001):

$$\mathrm{n}(t+1) = \mathbf{A}\mathrm{n}(t) \qquad (1)$$

where the vector $\mathrm{n}(t)$ represented the number of plants in four discrete life stages at time t and $\mathrm{n}(t+1)$ was the number of plants in each life stage the following year. The transition matrix **A** was composed of eight non-zero matrix elements (a_{ij}), which represented the transition probabilities of the seedling (*s*), small immature (*si)*, large immature (*li)*, and mature (*m*) life stages from time *t* to *t* +1. Unobserved transitions over the study period were represented in matrix **A** as zeros:

$$\mathbf{A} = \begin{pmatrix} \sigma_s(1-\gamma_s) & 0 & 0 & \varphi_m \\ \sigma_s\gamma_s & \sigma_{si}(1-\gamma_{si}) & 0 & 0 \\ 0 & \sigma_{si}\gamma_{si} & \sigma_{li}(1-\gamma_{li}) & 0 \\ 0 & 0 & \sigma_{li}\gamma_{li} & \sigma_m \end{pmatrix}$$

Matrix **A** was parameterized to include the probability of survival (σ_i), growth to the next stage class (γ_i), and fecundity (φ_m). Fecundity (φ_m) was calculated by dividing the number of seedlings counted in a given year by the number of mature plants the previous year. Matrix **A** captured the population demographic transitions under management of feral pigs and invasive plant competition while including frugivory by *L. lutea*. In 2011–2012, there was unintentional impact of herbicide drift on mature plants (based on qualitative field observations). Mature plants wilted and shed their leaves two weeks after the control of ecosystem altering vegetation, which occurred directly around the plants. For this reason, the 2011–2012 survival of matures ($\sigma_m = 47\%$) was lower than to the other transition years ($\sigma_m = 98\% - 81\%$). Since mortality from herbicide drift was not expected to occur in the future and we wanted to make our results were generalizable to other sites, we did not use the 2011–2012 σ_m data to calculate mature plant survival for the 2011–2012 matrix **A** transition year. Instead, we used the mean survival of mature plants in 2010–2011, 2012–2013, and 2013–2014 for the 2011–2012 matrix **A** σ_m term.

Simulating the effects of microhabitat heterogeneity and frugivory

Matrix **A** represents field microhabitat conditions while maintaining frugivory by *L. lutea*. To simulate the effects of changes in microhabitat heterogeneity and frugivory by *L. lutea* on the dynamics of the *C. dentata* population, we constructed three additional matrices **B**, **C**, and **D** by modifying matrix **A**. Based on the results of additional field

experiments, we found that frugivory by *L. lutea* and the availability of optimal microhabitat impacted the fertility φ_m of matrix **A** (see Appendix S1, A and B). To construct matrix **B**, which captures the removal of frugivory while maintaining field microhabitat conditions, we increased the φ_m element of matrix **A** by the percentage of fruits consumed by *L. lutea* at our field site. To construct matrix **C,** which represents the removal of frugivory and suboptimal microhabitat, we decreased the φ_m element of matrix **B** by the difference in seedling establishment between the optimal and suboptimal microhabitat. Lastly, to construct matrix **D**, which simulates the influence of both stressors (i.e., frugivory and suboptimal microhabitat), we decreased φ_m of matrix **A** by the percent difference in seedling establishment between the optimal and suboptimal microhabitat. Given the relatively short duration of the *C. dentata* fruiting season (i.e., three months), we assumed *C. dentata* germination and the number of seeds per fruit was not temporally variable.

Stochastic long-term population dynamics

For the four scenarios **A**, **B**, **C**, and **D** we projected the stochastic long-term population growth rate λ_s. To incorporate the effect of temporal variation in demographic processes to fluctuations in environmental conditions (i.e., environmental stochasticity) on population dynamics, we used the four years of demographic data to develop temporally varying stochastic matrix models for each scenario **A**, **B**, **C**, and **D** previously defined:

$$\mathrm{n}(t+1) = \mathbf{X}(t)\mathrm{n}(t) \qquad (2)$$

where $\mathbf{X}(t)$ is a random population projection selected at given time *t* from a pool of four yearly matrix transitions (2010–2011, 2011–2012, 2012–2013, and 2013–2014) for the

corresponding scenario (**A**, **B**, **C**, and **D**). The yearly matrices had an equal probability of being selected each iteration. The stable stage distribution (SSD) was used as the initial stage structure $\mathrm{n}(0)$. We assumed the time-varying model followed an identically independent distribution (*i.i.d*). For each scenario, we used equ 2 to calculate the stochastic growth rate λ_s with 95% confidence intervals by simulation using 50,000 iterations, following Tuljapurkar et al. (2003):

$$\log\boldsymbol{\lambda_s} = \lim_{t\to\infty}\left(\frac{1}{t}\right)\log[P(t)/P(0)] \qquad (3)$$

where $P(t)$ is the population size, i.e., the sum of the elements of $\mathrm{n}(t)$ at a given time t. Confidence intervals were calculated using a standard bootstrap approach, as outlined in (Morris and Doak, 2002, Caswell, 2001). To evaluate the individual and combined influence of microhabitat and seed consumption by *L. lutea* on population dynamics, we compared the λ_s of each scenario (**A**, **B**, **C**, and **D)**. To identify the relative importance of different life stages on the stochastic population growth rate λ_s for each scenario, we calculated the elasticity $E^{\mu S}$of λ_s to perturbation of mean matrix elements μ_{ij} following Tuljapurkar et al. (2003).

Stochastic short-term population dynamics

We calculated the stochastic short-term population growth rate for each management scenario **(A**, **B**, **C**, and **D)**, using the following formula:

$$r(t_1, t_{10}) = \frac{1}{t_{10}-t_1}\log\frac{N(t_{10})}{N(t_1)} \qquad (4)$$

The transient population growth rate was calculated as the average of a 1,000 independent sample paths of length t = 10 years. The stage structure at $\mathrm{n}(t+1)$ was calculated using equ 2. For a given year t $(t < 10)$, and for each management scenario,

we randomly selected one of the four yearly transition matrices (2010–2011, 2011–2012, 2012–2013, and 2013–2014) with equal probability to account for the effect of environmental variability. The timeframe of $t = 10$ years was used because it is the recommended timeframe to evaluate population dynamics of critically endangered plants by the IUCN red listing guideline (IUCN, 2001) and a reasonable length of time of a restoration management plan. Lower survival of mature plants in 2011–2012, due to herbicide drift, likely resulted in a lower proportion of individuals with high reproductive value in 2014 than would otherwise be expected. If the stage structure of the population had not been affected by herbicide drift, the short-term growth rate would likely have been slightly higher (i.e., population amplification) prior to SSD being achieved. However, in order to simulate short-term projections that could be used by conservation practitioners to manage the Kahanahāiki *C. dentata* population, we chose to use the observed population size in 2014 as the initial stage structure $\mathrm{n}(0)$.

To identify the relative importance of life stages on the short-term population growth rate, we conducted stochastic transient elasticity analyses with respect to small changes in matrix elements to unperturbed stage structure, $e_{1,i,j}$ (Haridas and Gerber, 2010, Haridas and Tuljapurkar, 2007). The $e_{1,i,j}$ distribution for each scenario ($\mathbf{A}, \mathbf{B}, \mathbf{C},$ and $\mathbf{D}$) was iteratively calculated by simulation, using 1,000 iterations. The four yearly transition matrices $\mathbf{X}(t)$ were selected with equal probability each iteration.

Results

Stochastic long-term population growth rates

The stochastic growth rate of the *C. dentata* population for scenario **A** (i.e., frugivory and field microhabitat conditions) was positive (λ_s = 1.032, 95% CI [1.028–1.037]), indicating a moderately growing population in the long-term (Figure 2.1a). Removal of frugivory by *L. lutea* while maintaining field microhabitat conditions (scenario **B)** increased the stochastic population growth rate by 1.7% (λ_s = 1.049, 95% CI [1.045–1.055]), relative to scenario **A** (Figure 2.1a). Maintaining frugivory while removing optimal microhabitat (scenario **C**) shifted the population growth rate from positive to negative (λ_s = 0.976, 95% CI [0.971–0.979]). The combined influence of both stressors (scenario **D**) decreased the stochastic population growth rate (λ_s = 0. 963, 95% CI [0.960–0.967]) and led to a declining population trajectory (Figure 2.1a).

Stochastic short-term population growth rates

Over the short-term, the *C. dentata* population was projected to grow moderately under current field conditions (i.e., frugivory and field microhabitat conditions) (r_s= 1.085, 95% CI [1.081–1.089]; Figure 2.1b). Similar to long-term projections, removal of frugivory increased the short-term population growth rate (r_s= 1.120, 95% CI [1.116–1.125]). Removal of optimal microhabitat reduced the short-term population growth rate (r_s= 0.984, 95% CI [0.980–0.987]). The combined impact of frugivory and the removal of optimal microhabitat had the greatest negative impact on the population growth rate (r_s= 0.960, 95% CI [0.952–0.960]).

Stochastic short and long-term elasticity

In the long-term, the survival of mature plants had the greatest proportional impact on the population growth rate, followed by the growth of seedlings, small immature, and large immature plants and fertility (Figure 2.2a). Removal of optimal

microhabitat for seedling establishment and frugivory increased the relative importance of the survival of mature plants on the long-term population growth rate. It also decreased the relative importance of the survival and growth of seedling, small immature, and large immature plants on the population growth rate (Figure 2.2a).

In the short-term, fecundity had the greatest relative importance on the population growth rate followed by the growth of seedlings to the small immature life stage (Figure 2.2b). The individual and combined impacts of seed consumption by *L. lutea* and removal of optimal microhabitat (scenario **A**, **C**, and **D**) reduced the relative importance of the fecundity and growth of seedlings to the small immature life stage (Figure 2.2).

Discussion

The influence of abiotic factors (e.g., light, soil type, elevation) on plant population dynamics has been well examined (Alvarez-Buylla et al., 1996, Brys et al., 2005, Colling and Matthies, 2006, Dahlgren and Ehrlén, 2009, Souther and McGraw, 2014). However, the influence of frugivorous animals or the combined effects of frugivory and microhabitat heterogeneity on plant population dynamics are rarely measured, and studies on this topic have produced mixed results (Godínez-Alvarez and Jordano, 2007, Loayza and Knight, 2010). Due to their adaptation to narrow ecological conditions and limited geographical distribution, localized endemics are likely to suffer stronger effects of such stressors. Thus, to fully understand the drivers of species decline, it is critically important to evaluate the individual and combined impact of environmental change, such as alterations in abiotic conditions and non-native frugivores, on the short-term (i.e., transient) and long-term (i.e., asymptotic) dynamics of rare species.

In this study, we found that rock outcrops (i.e., rocky gulch walls and small boulders in the gulch bottom) were an optimal microhabitat for *C. dentata* seedling establishment. Though the mechanism underpinning higher seedling establishment on rock outcrops is unknown, previous research suggests that rocks covered by moss can maintain a moist microsite favourable for seedling establishment (Ren et al., 2010). We also found that *C. dentata* seeds that were not contributing to local dynamics were consumed by *L. lutea* and dispersed away from the population. Under current field conditions (i.e., intensity of frugivory by *L. lutea* and microhabitat conditions at the field site), *C. dentata* was projected to persist in the long-term. Removal of frugivory moderately increased the long-term population growth rate, as compared to field conditions. Under suboptimal microhabitat conditions the long-term population growth rate was negative, regardless of frugivory pressure. These results suggest that for *C. dentata,* the removal of optimal microhabitat availability for seedling establishment would have a greater influence on population dynamics than frugivory by *L. lutea*. Furthermore, we found that the short-term transient growth rate (i.e., over 10 years) was slightly higher than the long-term growth rate. However, for each scenario, the projected direction of the short and long-term growth rates were not different. Additionally, there was more variation in the long-term projections than in the short-term projections (Figure 2.1). In the transient phase, the population dynamics are strongly influences by the initial condition of the population (Ellis and Crone, 2013). Conversely, the stochastic long-term dynamics are strongly influenced by variation in vital rates (Ellis and Crone, 2013). Thus, greater variation in long-term dynamic than in the short-term dynamics of *C. dentata* can

be explained, in part, by the effects of the year to year differences in targeted vital rates, after the strong effects of initial population structures has damped out. Though herbicide drift altered the stage structure of the population by decreasing the proportion of plants with high reproductive value, the population was still projected to persist in the short-term. If herbicide drift had not occurred, however, the population would likely have grown faster in the short-term (i.e., transient amplification), which is important to consider when evaluating the population dynamics of other *C. dentata* population not experiencing this demographic disturbance.

Dispersal agents can provide enemy escape from predators in close proximity to parent plants, reduce conspecific seedling competition, and increase seed germination for species reliant on gut passage to maintain high seed viability (Howe and Smallwood, 1982, Willson and Traveset, 2000). For species that produce more seeds than are needed to maintain a persistent population, dispersal away from geographically isolated populations can have a positive effect on metapopulation dynamics. However, for species on the brink of extinction the removal of seeds away from a population can shift the population trajectory from persistent to declining. In this study, we found that a majority of the seedlings at the field site either established slightly down gulch or underneath the crown of reproductively mature plants. This observation supports previous studies that suggest passive transport by water is a short-distance dispersal strategy for *Cyrtandra* species in Hawaii (Kiehn, 2001). We also found that seed germination from whole *C. dentata* fruits was relatively high, which suggest this taxon is not dependent on gut passage by frugivores to maintain high seed viability (see Appendix S1, Figure 2.2).

These results suggest *C. dentata* is not reliant on avian dispersal to maintain locally persistent populations.

Following massive extinction of native Hawaiian birds it is likely that many native species are dispersal limited, which may eventually reduce plant fitness by decreasing gene flow between populations. However, decreased gene flow between populations may be mitigated by cross-pollination between populations. For *C. dentata*, there is only five known extant populations, only two of which, Kahanahāiki and Pahole to West Makaleha, have > 16 mature plants and individuals in earlier life stages (i.e., immature plants and seedlings). Of those populations, Pahole to West Makaleha was the only population closer to Kahanahāiki (< 3 ha) than the home range of *L. lutea.* If rare long-distance dispersal between the Kahanahāiki and Pahole to West Makaleha populations is occurring by *L. lutea*, it may have an effect on plant fitness over time by increasing gene flow between populations. However, to fully understand the effect of rare long-distance dispersal would require a metapopulation approach, incorporating extinction and re-colonization events, and this is beyond the scope of this study.

For long-lived species, it is expected that later life stages will have a larger impact than earlier life stages on the long-term population growth rate (Silvertown et al., 1993, Haridas and Gerber, 2010). The importance of later life stages on population dynamics of long-lived species is commonly explained by life history strategy. High survival of mature plants can insulate long-lived species from environmental variability and thus is the most important vital rate for maintaining population persistence in the long-term.

However, recent research suggests that long-term elasticity does not always adequately describe the importance of life stages and associated vital rate in the short-term (Haridas and Gerber, 2010, Haridas and Tuljapurkar, 2007). In some scenarios, earlier life stages disproportionally contributed to the population growth rate of long-lived species over the short-term (e.g., 10 years), relative to later life stages (Gaoue, 2016, Haridas and Gerber, 2010, Haridas and Tuljapurkar, 2007, McMahon and Metcalf, 2008, Ezard et al., 2010a). Consistent with these studies, we also found a shift in the short and long-term elasticity patterns of the *C. dentata* population growth rate to perturbation of vital rates. *Cyrtandra dentata* long-term stochastic elasticity was dominated by the survival of mature plants. However, in the short-term, the establishment of *C. dentata* seedlings had the greatest influence on the population growth rate. These results have several management implications for *C. dentata*. First, with high mature plant survival (81% – 97%), there is likely little that can be done to improve that vital rate. However, the importance of mature plants on the long-term population growth rate emphasizes the gravity of maintaining high survival of matures over time. Secondly, management actions that increase seedling establishment would have the greatest positive impact on the population growth rate in the short-term.

Studying the demography of rare and endangered species is challenging due to limited replication (Morris and Doak, 2002). Despite the constraint of limited replication valuable insight can be gained from population dynamic studies of endangered species, such as quantifying the likely outcome of management actions and assessing the potential impact of environment parameters on population dynamics (Dostálek and Münzbergová,

2013, Ellis et al., 2007, García, 2003, Marrero-Gómez et al., 2007, Crone et al., 2011, Morris et al., 2002). It can also provide a proactive method of predicting the likely outcome of management actions, which would otherwise take several generations to detect (Menges, 2000). For this study, we were limited to one study site because it was the only *C. dentata* population that was composed of more than several individual and we had permission to access. Thus, results from this study may not be extrapolated across varying habitat and ecological conditions. Future integrative studies on the combined impact of plant interactions with multiple environmental parameters would benefit from having replication across multiple study sites. Plant population response to environmental stressors should be studied for more species varying in life history in order to investigate if generalized patterns emerge, which could be used to effectively manage rare plants and the habitat that they depend on.

Regardless of the difficulties of studying endangered species, the results of this study emphasize the importance of protecting optimal microhabitat for seedling establishment to maintain a positive population trajectory for endangered species that are sensitive to fine-scale environmental change. For *C. dentata*, a management strategy that would prevent degradation of optimal abiotic conditions for seedling establishment is the suppression of competitive vegetation. One of the most invasive ecosystem altering species at Kahanahāiki is *Blechnum appendiculatum*, which is a non-native fern that forms large clonal colonies and prevents germination of many native species in Hawaii (Wilson, 1996). *Blechnum appendiculatum* has started to encroach on rock outcrops at the Kahanahāiki *C. dentata* field site. If left uncontrolled, *B. appendiculatum* will

ultimately degrade optimal microhabitat for seedling establishment and negatively impact local population dynamics. The influence of fine-scale abiotic conditions on population dynamics also emphasizes the importance of selecting reintroduction sites with appropriate microhabitat for *C. dentata*, which will be necessary to delist this taxon following the United States Fish and Wildlife criteria (USFWS, 1998). The results of this study also illustrate that for localized endemic species on the brink of extinction, such as *Cyrtandra dentata,* non-native frugivores can reduce local seedling recruitment of geographically isolated populations. In combination with other environmental stressors, such as degradation of abiotic conditions, frugivory by non-native birds can shift the population growth rate of endangered plants from growing to declining over time.

Data accessibility

Matrices used to simulate short and long-term population dynamics of each scenario are deposited in Dryad (Bialic-Murphy et al., 2016).

Supporting information

Appendix S1, A: Results of frugivory by *Leiothrix lutea* and B: Results of microhabitat heterogeneity.

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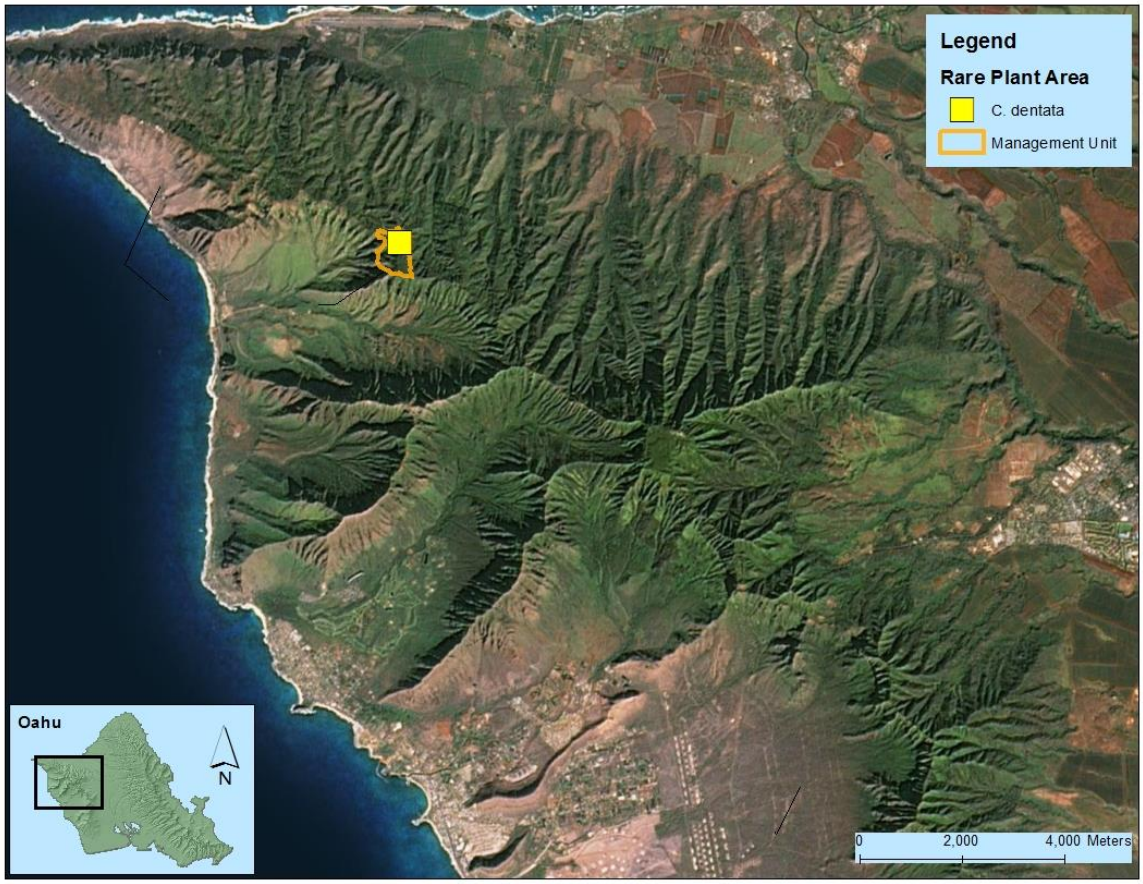
Table 2. 1 Location of a single population of *Cyrtandra dentata* in the Kahanahaiki Management Unit, in the northern Waianae Mountain Range of Oahu.



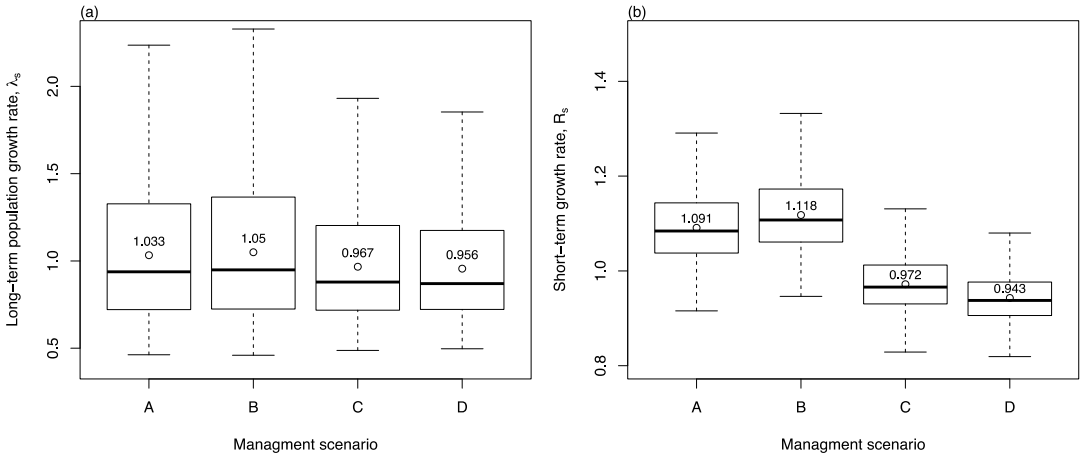


Figure 2. 1 Stochastic short ($\boldsymbol{R_s}$) and long-term ($\boldsymbol{\lambda_s}$) population growth rates of *C. dentata*. The black bar is the median and the boxes represent the inter-quartile range. The limits of the whiskers are 1.5 x the inter-quartile range. The open circle is the mean of each management scenario. Scenario A = Field conditions (i.e., field microhabitat conditions and frugivory), B = No frugivory while maintaining field microhabitat conditions, C = No frugivory and suboptimal microhabitat, D = Frugivory and suboptimal microhabitat.

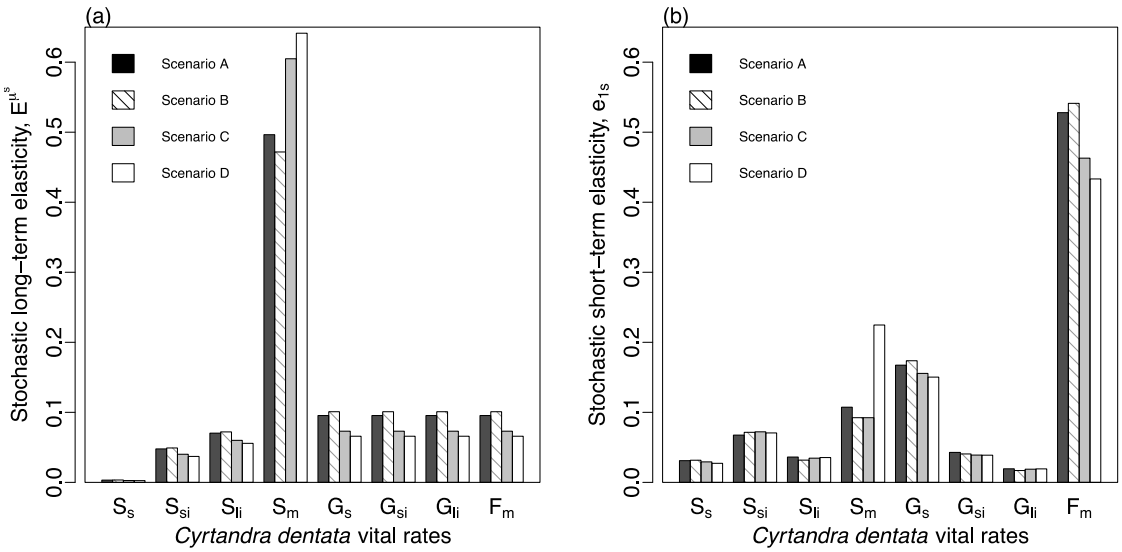


Figure 2. 2 Stochastic elasticities of *C. dentata* (a) long- and (b) short-term growth rates to perturbation of mean vital rates. The vital rates are survival (**S**), growth (**G**), and fertility (**F**) and the life stages are seedling (*s*), small immature (*si*), large immature (*li*), and mature (*m*). Scenario A = Field conditions (i.e., field microhabitat conditions and frugivory), B = No frugivory while maintaining field microhabitat conditions, C = No frugivory and suboptimal microhabitat, D = Frugivory and suboptimal microhabitat

Supporting information for

Microhabitat heterogeneity and a non-native avian frugivore drive the population dynamics of an island endemic shrub, *Cyrtandra dentata*

Appendix S1

A: Results of frugivory by *Leiothrix lutea*

To identify all potential avian frugivores consuming *C. dentata* fruits, we installed four day/night still image cameras (Moultrie Game Spy D40, Moultrie Products, LLC, Alabama, USA) at the study site during the peak *C. dentata* 2011 fruiting season. Each still image camera was attached to a stake, positioned 2 meters away from a mature plant, and focused on fruiting branches. The cameras were checked once a week for one month from mid-August to mid–September 2011, capturing frugivory visitation for approximately 33% of the 2011 *C. dentata* fruiting season. The images were reviewed, and fruit visitation was recorded. Since the objective of installing the image cameras was to identify all potential avian frugivores, we disregarded images triggered by wind and human movement. It is important to note that there are smaller birds than *L. lutea* that occur at the field site, including *Zosterops japonicus* and *Chlorodrepanis virens*. However, these avian dispersal agents would have been captured using the still image cameras if they had visited the monitored *C. dentata* plants (Sean E. MacDonald, unpublished data). During the fifteen monitoring dates, *L. lutea* was the only frugivore photographed. Thus, we assumed *L. lutea* was the only frugivore consuming *C. dentata* fruits that had a quantitatively important effect on local population dynamics. Since *L. lutea* is a generalist bird that is highly nomadic during peak *C. dentata* fruiting season

(Male et al., 1998) and the small geographical size of the *C. dentata* population (i.e., 150 long x 5 meters wide), we assumed 100% of the consumed fruits were dispersed away from the population. This assumption was supported by surveys at the field site, where we observed *L. lutea* flying into the gulch in flocks, moving through the understory for short periods of time, and then flying out of the study site. Our observations were similar to previous studies of *L. lutea* flight patterns (Male et al., 1998).

To measure the effect of frugivory by *L. lutea* on the *C. dentata* population dynamics, we randomly selected 11% of the mature plants at the site (i.e., five mature plants). On each plant, four mature fruits were tagged and monitored for a month, starting in mid-August of 2011. To identify the fruits in subsequent visits, we tied orange thread to the petiole of each fruit. We identified the animal species that consumed the fruit by examining the incisor marks on the remaining pericarp (Figure S2.1). When the fruits were consumed by *L. lutea*, the small *C. dentata* seeds (ca. 0.5 mm) in the fleshy fruits were also ingested. The total number of consumed fruits was counted each visit. Fruits that were not consumed following maturation and abscission from the plant were found on the forest floor with the orange string still attached. We used these data to estimate the percentage of fruits consumed.

For this field study, we found that 20% of the monitored fruits were consumed. The observed incisor lacerations on the remaining pericarp of mature fruits were indicative of bird consumption (Figure S2.1). Given that the *L. lutea* was the only frugivore detected perching on *C. dentata*, using the infrared image cameras, we assumed

it was the culprit of all fruit consumption. We assumed the percentage of seeds consumed was directly proportional to the percentage of fruits removed from the population. These data were used to assess the impact of *L. lutea* on the short-term and long-term *C. dentata* population dynamics (see section: *Simulating the effects of microhabitat heterogeneity and frugivory).*

B: Results of microhabitat heterogeneity

Preliminary field observations suggested that *C. dentata* recruit preferentially on rocky gulch walls and boulders in the gulch bottom, relative to soil. To quantify the influence of microhabitat heterogeneity on plant vital rates and population dynamics of *C. dentata*, we first classified microhabitats as optimal (i.e., boulders in the gulch bottom and rocky gulch walls) and suboptimal (i.e., soil). Then, we collected additional field data to determine the probability of survival, growth, and fertility on those two discrete microhabitats. To quantify potential differences in survival and growth for each life stage by microhabitat, we recorded the rooting substrate for each tagged plants from 2010–2014. To evaluate the effect of microhabitat on seedling establishment, we first quantified the proportion of the study site that was covered by each microhabitat by installing ten 1m x 1m quadrats directly underneath randomly selected mature plants (representing 22% of the mature plants in 2010-2011). These randomly selected quadrats spanned the length of the gulch, capturing the spatial distribution of the *C. dentata* population. For each quadrat, we recorded the total number of seedlings established and visually estimated the percent cover of rock outcrops and soil. These data were then used to calculate the expected and observed seedling establishment rates by microhabitat. We

assumed the percentage of total seedlings that established on each microhabitat would be equal to the percent cover by microhabitat, if there were no difference in microhabitat suitability. The difference in the expected and observed establishment rates of seedling by microhabitat were used to assess the effects of microhabitat heterogeneity.

In this field study, we found that seedling establishment was 65% greater on rock outcrops than on soil ($\chi^2 = 18$, $P < 0.0001$). However, the other life stages and associated vital rates did not differ significantly between rock outcrops and soil. These results suggest that the fine-scale patchy distribution of *C. dentata* plants was driven by differences in seedling establishment and rock outcrops was an optimal microhabitat for seeding establishment. These data were used to simulate the impact of microhabitat heterogeneity on the short-term and long-term *C. dentata* population dynamics.

Figure S2. 1 Typical laceration markings on the remaining pericarp of mature *C. dentata* fruits. Incisor marks (white arrows) are indicative of fruit consumption by birds. The subset of tagged fruit likely consumed by *L. lutea*, given they were the only animal detected perching on *C. dentata* by the infrared image cameras.

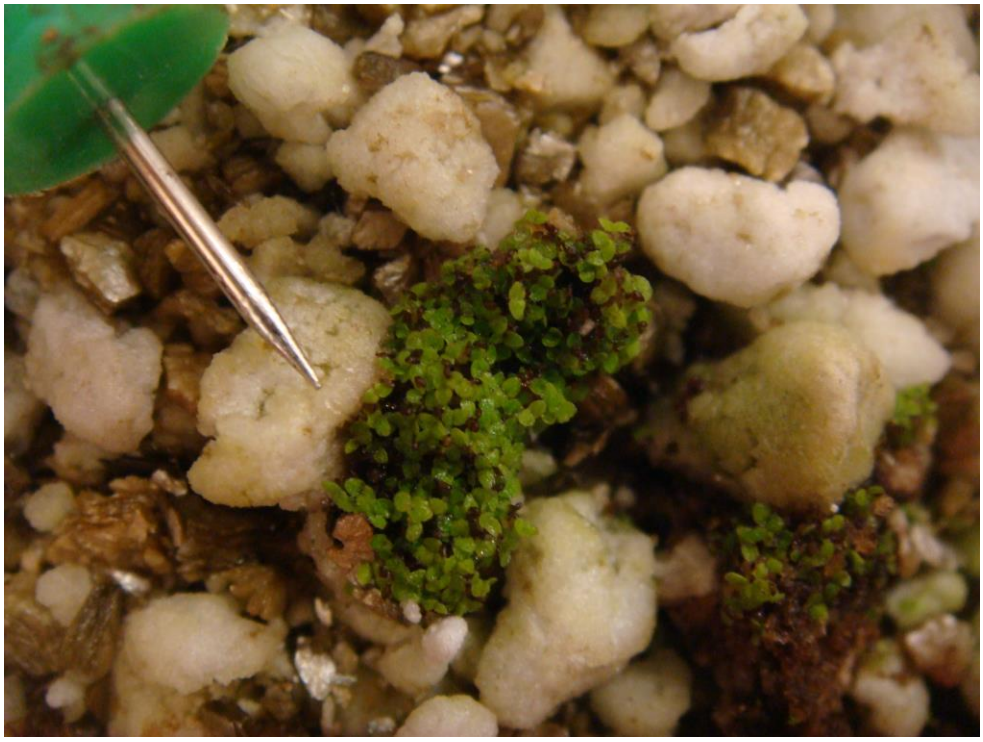


Figure S2. 2 Seedling germination from a mature *C. dentata* fruit when places on a mist bench in a greenhouse.

SimulationA_2010_2011				
	seedling	smallimm	lgimm	mature
seedling	0.090	0.0000	0.000	13.330
smallimm	0.109	0.5600	0.000	0.000
lgimm	0.000	0.0195	0.385	0.000
mature	0.000	0.0000	0.385	0.979

SimulationA_2011_2012				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	4.44
smallimm	0.507	0.372	0.000	0.00
lgimm	0.000	0.235	0.500	0.00
mature	0.000	0.000	0.303	0.87

SimulationB_2010_2011				
	seedling	smallimm	lgimm	mature
seedling	0.090	0.000	0.000	15.996
smallimm	0.109	0.560	0.000	0.000
lgimm	0.000	0.02	0.385	0.000
mature	0.000	0.000	0.385	0.979

SimulationB_2011_2012				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	5.328
smallimm	0.507	0.372	0.000	0.000
lgimm	0.000	0.235	0.500	0.000
mature	0.000	0.000	0.303	0.870

SimulationC_2010_2011				
	seedling	smallimm	lgimm	mature
seedling	0.090	0.000	0.000	5.986
smallimm	0.109	0.560	0.000	0.000
lgimm	0.000	0.020	0.385	0.000
mature	0.000	0.000	0.385	0.979

SimulationC_2011_2012				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	1.865
smallimm	0.507	0.372	0.000	0.000
lgimm	0.000	0.235	0.500	0.000
mature	0.000	0.000	0.303	0.870

SimulationD_2010_2011				
	seedling	smallimm	lgimm	mature
seedling	0.090	0.000	0.000	4.479
smallimm	0.109	0.560	0.000	0.000
lgimm	0.000	0.020	0.385	0.000
mature	0.000	0.000	0.385	0.979

SimulationD_2011_2012				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	1.492
smallimm	0.507	0.372	0.000	0.000
lgimm	0.000	0.235	0.500	0.000
mature	0.000	0.000	0.303	0.870

SimulationA_2012_2013				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	2.000
smallimm	0.322	0.157	0.000	0.000
lgimm	0.000	0.137	0.500	0.000
mature	0.000	0.000	0.250	0.890

SimulationA_2013_2014				
	seedling	smallimm	lgimm	mature
seedling	0.103	0.000	0.000	3.430
smallimm	0.118	0.265	0.000	0.000
lgimm	0.000	0.190	0.444	0.000
mature	0.000	0.000	0.167	0.810

SimulationB_2012_2013				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	2.400
smallimm	0.322	0.157	0.000	0.000
lgimm	0.000	0.137	0.500	0.000
mature	0.000	0.000	0.250	0.890

SimulationB_2013_2014				
	seedling	smallimm	lgimm	mature
seedling	0.103	0.000	0.000	4.012
smallimm	0.118	0.265	0.000	0.000
lgimm	0.000	0.190	0.444	0.000
mature	0.000	0.000	0.167	0.810

SimulationC_2012_2013				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.000	0.840
smallimm	0.322	0.157	0.000	0.000
lgimm	0.000	0.137	0.500	0.000
mature	0.000	0.000	0.250	0.890

SimulationC_2013_2014				
	seedling	smallimm	lgimm	mature
seedling	0.103	0.000	0.000	1.404
smallimm	0.118	0.265	0.000	0.000
lgimm	0.000	0.190	0.444	0.000
mature	0.000	0.000	0.167	0.810

SimulationD_2012_2013				
	seedling	smallimm	lgimm	mature
seedling	0.010	0.000	0.00	0.672
smallimm	0.322	0.157	0.00	0.000
lgimm	0.000	0.137	0.50	0.000
mature	0.000	0.000	0.25	0.890

SimulationD_2013_2014				
	seedling	smallimm	lgimm	mature
seedling	0.103	0.000	0.000	1.123
smallimm	0.118	0.265	0.000	0.000
lgimm	0.000	0.190	0.444	0.000
mature	0.000	0.000	0.167	0.810

Figure S2. 1 Yearly transition matrices for each simulation from 2010-2014. Scenario A = Field conditions (i.e., field microhabitat conditions and frugivory), B = No frugivory while maintaining field microhabitat conditions, C = No frugivory and suboptimal microhabitat, D = Frugivory and suboptimal microhabitat.

Chapter 3 Low inter-annual precipitation has a greater negative effect than seedling herbivory on the population dynamics of a short-lived herb, *Schiedea obovata* (Caryophyllaceae)

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Running title: Precipitation, herbivory, and plant demography

Keywords: integral projection model, *Schiedea obovata*, plant reintroduction, restoration ecology, endangered species, inter-annual precipitation, life table response experiment (LTRE), mollusc herbivory, temporal variability, plant-climate interactions, plant-animal interactions.

Abstract

1: Climate projections forecast more extreme inter-annual climate variability over time, with an increase in the severity and duration of extreme drought and rainfall events. Based on bioclimatic envelope models, it is projected that changing precipitation patterns will drastically alter the spatial distributions and density of plants and be a primary driver of biodiversity loss. However, many other underlying mechanisms, such as the introduction of non-native seedling herbivores, can also impact plant vital rates (i.e., survival, growth, and reproduction) and population dynamics.

2: In this study, we used a size dependent integral projection model (IPM) to evaluate how inter-annual precipitation and mollusc herbivory influenced the temporal variability in the dynamics of a Hawaii endemic short-lived herb, *Schiedea obovata* (Caryophyllaceae).

3: Wet season precipitation had a greater effect on population growth rate of *S. obovata* than mollusc herbivory and the impact of precipitation on plant vital rates shifted across plant ontogeny. Furthermore, wet season precipitation influenced multiple vital rates in contrasting ways and the effect of precipitation on the survival of larger vegetative and reproductively mature individuals contributed the most to variation in the population growth rate λ. We also found a synergistic effect of precipitation and herbivory, with a greater negative effect of herbivory on population growth rate λ in years with high wet season precipitation.

4: *Synthesis and application*. Our study highlights the importance of evaluating how abiotic factors and plant-consumer interactions influence an organism across its life cycle to fully understand the underpinning mechanisms that structure its spatial and temporal distribution and abundance. Our results also illustrate that the effect of plant-herbivore interactions on plant population dynamics is context specific and for short-lived species, like *S. obovata*, seedling herbivores can have less of an effect on the dynamics of plant populations than abiotic conditions.

Introduction

Plant endangerment is driven by complex interactions of multiple environmental stressors, which can have varying effects on plant vital rates and ultimately population dynamics (Brook et al., 2008). Two of the primary environmental stressors implicated in the decline of species globally are changing precipitation patterns and the introduction of non-native herbivores (Parmesan, 2006, Wilcove et al., 1998). The independent influences of these environmental stressors on various components of plant fitness (e.g., survival and growth) have been well examined and often used to prioritize restoration actions (Hanley et al., 1995, Joe and Daehler, 2007, Orians et al., 2013, Parmesan, 2006, Cowie et al., 2009). From those studies, we have gained an in-depth understanding of the direct impacts of various environmental stressors on the vital rates of native species. However, comparing the effects of different environmental stressors on components of plant fitness can be a poor predictor of which environmental stressors will have the greatest effect on population growth rate (Ehrlén, 2003).

A small, but growing, body of literature shows that the effect of environmental stressors on population dynamics is context specific (Miller et al., 2009, Dahlgren and Ehrlén, 2009, Gaoue et al., 2011, Gaoue and Ticktin, 2010). There is also clear evidence that the effect of environmental stressors on plant population dynamics is driven, in part, by their life history strategy (Crone et al., 2013, MorrisPfister et al., 2008, Dalgleish et al., 2010). Climate projection models suggest that large-scale environmental change has already directly affected the phenology and geographical range of Earth's flora and fauna (Guisan and Thuiller, 2005). It is predicted that environmental conditions will continue to

drastically alter species' distributions, as variation in inter-annual environmental conditions increase (Williams et al., 2007). A primary assumption of those studies and future projections of the influence of environmental change on species' climate envelope (i.e., projected distribution models) is that abiotic parameters, including precipitation, are strong drivers of the spatial distribution and abundance of plants (Guisan and Thuiller, 2005). However, climate change can have varying effects on plant vital rates across ontogeny, sometimes in opposite directions. There are also many other underlying mechanisms, such as plant-consumer interactions, that can influence the spatial distribution and abundance of plants along an elevation gradient (Miller et al., 2009). Surprisingly, few studies have evaluated how changes in precipitation influence the full life cycle of plants and quantified how precipitation drives spatial and temporal variation in population dynamics (but see, Dalgleish et al., 2010, Dalgleish et al., 2011, Jongejans et al., 2010, Salguero-Gómez et al., 2012, Tye et al., 2016).

In addition to changes in climate, selection pressures such as non-native herbivores are critical drivers of species endangerment and exogenous determinants of plant fitness and evolutionary potential. Due to the lack of diverse herbivore communities on islands, many species native to remote islands have lower mechanistic and physiologic tolerance to non-native herbivores than continental relatives (Bowen and Vuren, 1997, Vitousek, 1988, Vourc'h et al., 2001, Carlquist, 1974). Thus, non-native herbivores may have a disproportionally large effect on spatial distribution and abundance of island species. Selection pressure by herbivores can lead to increased plant tolerance and resilience in subsequent generations (Orians et al., 2013). At the community level,

herbivores can decrease plant diversity (Hanley et al., 1995). Most herbivore-plant interaction studies, however, have not explicitly evaluated how changes in various measures of plant vital rate (e.g., survival, growth, and reproduction) influence the overall population dynamics (but see, Miller et al., 2009, Ehrlen, 1995b, Ehrlen, 1995a, Maron and Crone, 2006). Of the studies that have been conducted to evaluate the population level effects of plant-herbivore interactions most have focused on vertebrates and insects, which primarily reduce vegetative biomass of later life stages (e.g., adults) and fertility respectively (Maron and Crone, 2006). There is also a small, but growing, body of literature that highlights how plant-herbivore interactions can vary along spatial and temporal abiotic gradients, suggesting plant-herbivore interactions are context specific (Miller et al., 2009, Dahlgren and Ehrlén, 2009).

Some of the most ubiquitous herbivores implicated in the decline of species globally, particularly on tropical oceanic islands, are non-native molluscs (Joe and Daehler, 2007, Lowe et al., 2000, Cowie et al., 2009). Molluscs primarily influence plant vital rates of earlier life stages (i.e., seedling establishment and survival), consuming meristematic tissue and foliage at the ground level (Barker, 1989, Byers and Bierlein, 1982). Following mollusc suppression, seedling establishment and density can increase significantly (Hanley et al., 1995, Joe and Daehler, 2007, Ehrlén, 2003). Interestingly, mollusc herbivory can have a larger effect on population growth rate than vertebrate grazers and pre- and post-seed predators (Ehrlén, 2003, Ehrlen, 1995a, Ehrlen, 1995b). However, there is a paucity of studies that have explicitly evaluated how mollusc

herbivory influences the dynamics of plant populations and this limits our ability to make guild-specific comparisons.

Prior demographic studies suggest that exogenous stressors that decrease vital rates of early life stages, such as seedling establishment, will have a greater negative impact on the population growth rate of short-lived species compared to long-lived species (Dalgleish et al., 2010, Silvertown et al., 1993). The greater relative importance of earlier life stages on the population dynamics of short-lived species is due to the limited number of years short-lived species have to successfully reproduce and replace themselves, relative to long-lived species (Silvertown et al., 1993). Consequently, short-lived species are also likely to be more susceptible to increased variability in environmental conditions and disproportionally threatened by climate change and non-native seedling herbivores than long-lived species (Crone et al., 2013, Dalgleish et al., 2010, MorrisPfiser et al., 2008).

In this study, we constructed a precipitation and herbivory dependent integral projection model (IPM) to investigate how precipitation and seedling herbivory by non-native molluscs (*Stylommatophora*, Limacidae and *Systellommatophora*, Veronicellidae) affect the temporal variation in the dynamics of a reintroduced population of a short-lived Hawaiian endemic herb, *Schiedea obovata* (Caryophyllaceae). Total annual precipitation can mask the effect of seasonal inter-annual precipitation on plant vital rates (i.e., survival, growth, and fertility). For this reason, we focused on evaluating the effect of temporal variation in wet season precipitation (October – March), when the focal taxon,

S. obovata, is fruiting, seedlings are establishing, and most vegetative growth occurs. To assess how wet season precipitation and herbivory influence the population dynamics of *S. obovata* we asked the following questions: (i) How does wet season precipitation and herbivory influence *S. obovata* vital rates and population growth rate? (ii) Is the effect of herbivory on population dynamics context specific, based on abiotic conditions? (iii) What demographic processes (i.e., survival, growth, and fertility) drive differences in population growth rates between years that vary in total wet season precipitation?

Material and methods

Study species

Schiedea obovata is a suberect or ascending Hawaii endemic short-lived, perennial, woody herb, reaching 0.3–1 m tall (WagnerWeller et al., 2005a). Fruits are capsules and the sepals are fleshy and dark purple. The pollen:ovule ratio of 310 for *S. obovata* indicates its breeding system is somewhere between facultative autogamy and xenogamy (WagnerWeller et al., 2005b). The purple berries it produces are indicative of frugivorous bird dispersal. *Schiedea obovata* fruits and flowers at the end of the wet season from February – May and seedlings establish the following wet season from December – March. The historical range of *S. obovata* spanned the Waianae Mountain Range, on the island of O'ahu, Hawai'i where it is confined between 550–800 m elevation, primarily along mesic ridgelines (Wagner et al. 1999). Over the past several decades *S. obovata* has experienced a severe reduction in geographical range and by 1991 it was listed as federally endangered (USFWS, 1991).

Study site and reintroduction details

The study site was a reintroduced population of *S. obovata* that is located in the Kahanahaiki Management Unit (36 ha), referred to hereafter as Kahanahaiki, which is in the northern Waianae Mountain Range, on the island of O'ahu (21° 32' N, -158°12' W) (Table 3.1). Kahanahaiki is a tropical mesic forest; composed of a mix of native and non-native flora and fauna. In 1996, prior to reintroduction, the O'ahu Army Natural Resources Program (OANRP) constructed the Kahanahaiki fence and controlled non-native ungulates. From 1999 to 2011, a total of six *S. obovata* outplanting efforts were undertaken and 258 individuals were reintroduced. Since 1998 OANRP has been conducting ecosystem level management for the protection of *S. obovata* and eleven other endangered species (OANRP, 2009), which includes the control of a non-native rodent *Rattus rattus* and bi-annual weed control of competitive ecosystem altering vegetation. Starting in 2011, localized suppression of non-native molluscs (*Stylommatophora*, Limacidae and *Systellommatophora*, Veronicellidae) has been executed at the reintroduction site. A monthly application rate of a molluscicide, Sluggo (Neudorff Co., Fresno, California), was used as the suppression methodology. Sluggo was not applied in the summer months, when slug herbivory was minimal (Stephanie Joe, pers. comm.).

The stock used for the Kahanahaiki *S. obovata* reintroduction came from a single founder that was found in close proximity to the reintroduction site. Site selection of the reintroduction was based on the following criteria: 1) appropriate habitat and associated species, 2) similar topography as naturally occurring populations and, 3) geographical proximity to naturally occurring *S. obovata* individuals (OANRP 2003a). Genetic stock

from the other six known populations was not used for the reintroduction to avoid potential outbreeding depression and the loss of localized adaptations (Kawelo et al. 2012). That decision was partially supported by recent research that examined the risk of inbreeding and outbreeding depression of mixing founder stock (Weisenberger, 2012). Inbreeding and outbreeding depression were not detected. However, plants from maternal source populations furthest from Kahanahaiki had the lowest progeny fitness when outplanted at Kahanahaiki. Given that Kahanahaiki was the driest and lowest elevation site that *S. obovata* had been documented from, reduced progeny fitness of plants from maternal source populations furthest from Kahanahaiki may indicate local adaptation. Alternatively, reduced progeny fitness may be the effect of the small population size and genetic drift. The management recommendation of Weisenberger (2012) for the reintroduction of *S. obovata* at Kahanahaiki was: "propagules that originate from higher elevations should not be moved to lower elevations. Kahanahaiki progeny are the only plants that should be planted into Kahanahaiki gulch." Seeds used for the reintroduction were collected and grown in a greenhouse for one growing season, prior to outplanting. The mean height of *S. obovata* when outplanted at Kahanahaiki was 58cm.

Demographic data

Demographic field monitoring was initiated in April of 2014 and was conducted annually for three consecutive years. Over the study period, we installed 18 1x1m permanent plots throughout the reintroduction field site and collected demographic data for a total of 422 individual plants. Plants in each plot that were > 8cm in height were permanently tagged. For plants <8cm, a subset of ten randomly selected plants was permanently tagged in each plot. To avoid damage, plants <8cm were marked using pin

flags and color coded wire. To evaluate the potential effect of density dependence on seedling vital rates, we assessed differences in the survival and growth of seedling clusters and isolated seedlings. For each tagged plant, we recorded its height to apical meristem, basal diameter, survival, and reproductive status (presence of flowers and fruits).

Construction of precipitation dependent vital rate functions

To explicitly evaluate the effects of wet season precipitation on the survival, growth, and fertility functions (see equations 2 and 3), we used a generalized linear mixed-effect model with precipitation and plant size at time t as predictor variables and plot and plant ID as random effects (Bolker et al., 2009). To investigate all potential effects and interactions of wet season precipitation and the associated vital rate predictor variables we used model selection, starting with a fully parameterized model and Akaike Information Criterion (AIC) to select the best supported models. To include all potential effects and interactions, we compared ΔAICc values and selected the most complex model with a ΔAICc < 2, where ΔAICc is the difference in AIC corrected for sample size between each candidate model and the model with the lowest AICc value. For the survival $s(x, a)$ model and the probability of fruiting function $f_f(x, a)$ of the fertility model we used a binomial error structure and for the growth model $g(y, x, a)$ we used a normal error structure. For the reproductive output function $p_r(a)$ (i.e., number of seedling per mature plant) of the fertility model, we used a negative binomial error structure to account for overdispersion.

The total wet season precipitation data (i.e., parameter a) that we used to evaluate

the effect of temporal variation in wet season precipitation on plant vital rates and population dynamics were collated from the National Oceanic and Atmospheric Administration for the Honolulu airport meteorological station 21.324° N and 157.929° W (NOAA Regional Climate Center, 2016). The first transition year 2014–2015 received average wet season precipitation (10.4 in) and the second transition year 2015–2016 was rated as a very strong (SST >2) El Nino Southern Oscillation Year and had lower than average wet season precipitation in Hawai‘i (5.99 in) (NOAA Regional Climate Center, 2016). For simplicity, hereafter the first transition year 2014–2015 is referred to as *high precipitation* and the second transition year 2015–2016 is referred to as *low precipitation*.

The best supported generalized linear mixed-effect models for survival $s(x, a)$ and probability of fruiting $f_f(x, a)$ were the most complex models, including initial size, wet season precipitation, and their interaction as predictor variables (Table 3.2). The best-supported model for plant growth $g(x, a)$ included the initial plant size as the predictor variable, suggesting that precipitation has little or no effect on growth within the bounds of precipitation that occurred over the study period 2014–2016 (Table 3.2). For the reproductive output function $p_r(a)$, the best-supported model was using wet season precipitation as the predictor variable (Table 3.2).

Effect of mollusc herbivory on S. obovata vital rates

To evaluate the effects of mollusc herbivory on the survival, growth, and fertility of *S. obovata,* we used a combination of field experiments. The effect of mollusc herbivory on seedling survival came from a previous field herbivory experiment that was conducted in close proximity to our field site (Kawelo et al., 2012). In that study, *S.*

obovata seeds were sown on the top layer of soil in 12 plots, 15m x 15m in diameter. Six of the plots were treated with molluscicide, Sluggo (Neudorff Co., Fresno, California) and the other six plots were left exposed to field herbivory conditions. Seedling density was recorded on a weekly basis for six weeks. The results of that study indicated that non-native molluscs had a significant effect on *S. obovata* seedling survival with 33% mean difference in seedling density by plot treatment (i.e., plots treated with molluscicide and plots exposed to natural field herbivory intensity). The height cutoff that we used to model the influence of herbivory on seedling survival was set to 2.4 cm because that was the mean height distribution of seedlings at time t+1.

To assess potential effects of herbivory on vital rates of plants > 2.4 cm, we recorded percent mollusc herbivory every six months over the course of our study. In total, we observed five tagged plants that were grazed by molluscs, only one of which was > 2.4 cm. All of the seedlings that were grazed died within the transition time t+1. The one grazed plant > 2.4 cm survived and had comparable growth to immature plants that were not grazed from time t to time t+1. With low observed mollusc grazing for plant > 2.4 cm, for our model simulations we made the assumption that mollusc grazing had little or no effect on vital rates of plants > 2.4 cm.

Integral projection model

To evaluate the effect of wet season precipitation and mollusc herbivory on *S. obovata* population dynamics, we developed a continuous size dependent integral projection model (IPM) (Easterling et al., 2000), which includes wet season precipitation, a, as a covariate:

$$\mathrm{n}(y, a, t+1) = \int_{\Omega} \mathrm{k}(y, x, a)\mathrm{n}(x, a, t)dx \quad (1)$$

where, the vector $\mathrm{n}(y, a, t+1)$ represents the number of individuals of size y at time $(t+1)$. The vector $\mathrm{n}(x, a, t)$ summarized the population state at time t. The k kernel is the nonnegative surface of all possible transitions (i.e., survival, growth, and fecundity) of individual plants from size x at time t to size y at time $(t+1)$, which was composed of two functions, survival-growth function $\mathrm{p}(y, x, a)$ and fertility $\mathrm{f}(y, x, a)$.

The survival-growth function $\mathrm{p}(y, x, a)$ represents the probability that individuals of size x survives $s(x, a)$ and grows $g(y, x, a)$ to size y:

$$p(y, x, a) = s(x, a)g(y, x, a) \quad (2)$$

The fertility function $\mathrm{f}(y, x, a)$ was calculated using the following equation:

$$f(y, x, a) = s(x, a)f_f(x, a)f_n(x, a)p_g p_e(x, a)\, f_d(y) \quad (3)$$

where $s(x, a)$ is the probability of mature plant survival, $\mathrm{f_f}(x, a)$ is probability of fruiting, $f_d(y)$ is the size distribution of seedlings, $f_n(x, a)$ is the number of fruits produced, and $\mathrm{p_g p_e}(a)$ is the probability of germination and seedling establishment. For our model we combined $f_n(x, a)$ and $p_g p_e(a)$ to capture reproductive output in terms of number of seedlings produced per mature plant, which is referred to as $p_r(a)$.The kernel k is integrated numerically over all possible plant height Ω, using the mid-point rule (Ellner and Rees, 2006). The result is a large matrix of 150 x 150 k, which has mathematical properties similar to matrix projection models (see Caswell 2001). The dominant eigenvalue of k represents the long-term population growth rate λ, which was calculated using the popbio package in R version 3.1.0 (Stubben and Milligan, 2007).

To evaluate the effects of density dependence on plant vital rates, we categorized the tagged plants as either isolated seedlings or seedling clusters. We then tested if there was a significant difference in the size-dependent survival and growth for these two categories. We assumed lower survival rate or slower growth of seedlings in clusters than isolated individual seedlings would indicate density dependence. However, we found no significant differences in vital rates of seedlings in clusters and isolated individual seedlings. Therefore, we developed our model without including density dependence.

Since wet season precipitation influenced multiple vital rates, we also conducted a retrospective life table response experiment (LTRE) analysis to identify the size dependent contribution of vital rates to a decrease in population growth rate λ in years with low wet season precipitation, relative to years with high wet season precipitation. The kernel of vital rates contributions C^d was calculated (Caswell, 2001, Elderd and Doak, 2006):

$$C^d = D^d \circ S_{k^i} \quad (4)$$

where D^d is the difference between the high precipitation and low herbivory kernel K^{HP-LH} and the low precipitation and low herbivory kernel K^{LP-LH}. The S_{k^i} kernel represents the sensitivity of the 'midway' kernel between K^{HP-LH} and K^{LP-LH}.

Simulations of population dynamics under varying levels of precipitation and herbivory

The IPM model described above in Eqn 1 was used to project the population dynamics for four scenarios: **1**) high wet season precipitation and low herbivory, **2**) high wet season precipitation and high herbivory, **3**) low wet season precipitation and low

herbivory, and **4**) low wet season precipitation and high herbivory. Hereafter the four scenarios are abbreviated as HP-LH, HP-HH, LP-LH, LP-HH, respectively.

For the high precipitation models (HP-LH and HP-HH) and low precipitation models (LP-LH and LP-HH**)**, we set the precipitation parameter a in our IPM kernel (Eqn 1) to 10.4 in and 5.99 in, respectively. High precipitation models were based on total observed wet season precipitation in 2014 – 2015 and the low precipitation models were based on the 2015 – 2016 El Nino Southern Oscillation year. To model the effect of mollusc herbivory on population dynamics, we manipulated seedling survival $s(x, a)$ of the constructed $\mathrm{p}(y, x, a)$ function of our IPM kernel (i.e., plants < 2.4 cm). For the high herbivory models (HP-HH and LP-HH), we decreased the $s(x, a)$ function of the low herbivory models (HP-LH and LP-LH) by 33%, based on the mollusc suppression using Sluggo. As previously mentioned, the proportional decrease in seedling survival $s(x, a)$ of the survival-growth function $\mathrm{p}(y, x, a)$ used for the high herbivory models (HP-HH and LP-HH) were based on the results reported in Kawelo et al. (2012).

Results

Effect of precipitation and herbivory on vital rates

Mollusc herbivory reduced seedling survival and wet season precipitation and plant size influenced survival, growth, and fertility in contrasting ways (Figure 3.1). The probability of fruiting increased with precipitation and plant size. Wet season precipitation had a greater effect on the probability of fruiting for larger plants than for smaller plants. The total number of seedlings per mature plant also increased with precipitation but was not influenced by plant size. Two of the plots in 2014 and three of

the plots in 2015 contained multiple reproductively mature plants. For these plots we divide the total number of seedlings by the total number of reproductively mature plants the previous year to calculate $p_r(a)$, which could have masked the influence of plant size on fertility. We found an interactive effect of plant size and precipitation on survival. Larger plants had higher probability of surviving than smaller plants. Wet season precipitation had mixed effects on survival. With increasing wet season precipitation, the probability of survival increased for large vegetative and reproductive plants but decreased for smaller plants (i.e., seedling) (Figure 3.1).

Population growth rates for varying levels of precipitation and herbivory

Decreased wet season precipitation had a greater negative effect on *S. obovata* population dynamics than mollusc herbivory (Figure 3.2). The population growth rates λ of the four scenarios, HP-LH, HP-HH, LP-LH, LP-HH, ranged from 1.032 to 0.828 respectively (Figure 3.2). The population growth rate of the HP-LH scenario was the highest ($\lambda_{HP\text{-}LH} = 1.032$), followed by the HP-HH scenario ($\lambda_{HP\text{-}HH} = 0.979$). The low precipitation scenarios (LP-LH and LP-HH) had the lowest population growth rates, ranging from $\lambda_{LP\text{-}LH} = 0.86$ to $\lambda_{LP\text{-}HH} = 0.828$. The only scenario that had a population growth rate > 1 was the HP-LH scenario (Figure 3.2). Furthermore, mollusc herbivory had a greater affect on population growth rate in years with high wet season precipitation than years with low wet season precipitation. We also found that the demographic processes that contributed the most to a decrease in the population growth rate λ in years with low wet season precipitation was a decrease in the survival of larger vegetative and reproductively mature plants, followed by a decrease fertility and an increase in shrinkage of small vegetative plants (Figure 3.3).

Discussion

The effects of environmental stressors on components of plant fitness (e.g., survival and growth) have been well examined (Hanley et al., 1995, Joe and Daehler, 2007, Orians et al., 2013, Parmesan, 2006, Cowie et al., 2009, Pender et al., 2013, Shiels and Drake, 2011). These studies provide insight into the effects of environmental stressors on susceptible vital rates. With this information alone, however, it is impossible to untangle which environmental stressors contribute the most to population decline and species endangerment. For short-lived organisms, such as *S. obovata*, predictions from ecological synthesis and life history theory suggest that vital rates of earlier life stages will have the greatest impact on population dynamics (e.g., population growth rate) (Silvertown et al., 1993, Stearns, 1992). As a result, it may be expected that environmental stressors that negatively affect earlier life stages will have the greatest negative effect on population dynamics of short-lived organisms. However, the influence of environmental stressors on population dynamics is dependent on: *which* vital rates are affected, the *magnitude* of change in susceptible vital rates, and the *sensitivity* of those vital rates on population growth rate (Caswell, 1989). Thus, in order to fully understand which environmental stressor or combination of stressors drive variation in population growth rate spatially and temporally requires a demographic model approach.

In this study, we found that wet season precipitation and initial plant size had varying effects on *S. obovata* vital rates. Wet season precipitation and initial plant size positively influenced survival and the probability of fruiting, with a higher probability of survival and fruiting for large reproductively mature plants than small reproductively mature plants. Consistent with previous studies, we found a positive relationship between

survival of later *S. obovata* life stages and precipitation (Dalgleish et al., 2011, Tye et al., 2016). Increased precipitation also had a positive influence on *S. obovata* seedling establishment. The influence of precipitation on the probably of fruiting and reproductive output are similar to results of previous studies (Kadmon, 1993). For earlier life stages (i.e., seedling and small vegetative plants), however, increased wet season precipitation reduced subsequent survival. The underpinning mechanism driving a negative influence of wet season precipitation on subsequent survival of early life stages is unknown. However, we offer a plausible explanation for this result. Previous research suggests that seedlings that established in low soil moisture conditions can have a higher root to shoot ratio than seedlings that establish in high soil moisture conditions (Sánchez-Blanco et al., 2009, Franco et al., 2008). As a result, seedlings that established in low soil moisture conditions can have higher subsequent survival and water use efficiency (Sánchez-Blanco et al., 2009, Franco et al., 2008). Vegetation flushes following high precipitation events can also intensify competitive interactions, which can lead to decreased seedling survival (Goldstein and Suding, 2014).

Based on previous studies of short-lived species, we predicted that vital rates of earlier life stages (e.g., seedling establishment and fertility) would contribute the most to lower population growth rate λ in years with low wet season precipitation (Dalgleish et al., 2010). Contrary to our expectation, however, we found that lower survival of larger vegetative and reproductively mature plants, lower fertility, and increased shrinkage of small vegetative plants contributed the most to a lower population growth rate in years with low precipitation (Figure 3.3). As illustrated by Figure 3.3, shrinkage of small

vegetative plants and lower fertility contributed moderately to lower population growth rate in years with low precipitation, whereas lower survival of larger vegetative and reproductively mature plants had the greatest contribution to lower population growth rate in years with low precipitation. This result illustrates the importance of evaluating the effect of environmental stressors on the full life cycle of an organism in order to fully understand if a targeted environmental stressor is a primary driver of population decline and extinction.

There is a small, but growing, number of studies that suggest that the effects of biotic stressors on population dynamics are dependent on local abiotic conditions (Dahlgren and Ehrlén, 2009, Miller et al., 2009). For example, Miller et al. (2009) found that insect herbivory was driving temporal variation in the population dynamics of a tree cactus, *Opuntia imbricata*, along an elevational gradient. Herbivory was also found to influence the variation in population dynamics between habitat types of an endangered herb, *Liatris ohlingerae*, with a greater effect of herbivory on population dynamics across habitat type in years with high precipitation (Tye et al., 2016). Similarly, the effect of harvesting non-timber forest products (i.e., reduction in foliar biomass) on the population dynamics of a long-lived tree, *Khaya senegalensis*, varied temporally along an elevational gradient. Regardless of harvest intensity (i.e., high and low), the population growth rate was > 1 in the wet region and <1 in the dry region (Gaoue and Ticktin, 2010). Furthermore, abiotic conditions were found to have a greater effect on *K. senegalensis* population dynamics than harvest intensity (Gaoue and Ticktin, 2010). Similar to previous studies we found that the effect of herbivory on population dynamics of *S.*

obovata was context specific, with a smaller effect of herbivory on population dynamics in years with low wet season precipitation than years with high wet season precipitation (Figure 3.2). As illustrated by the subadditive effect of herbivory on population dynamics in years with low wet season precipitation (Figure 3.2), organisms can reach a saturation point after which top down stressors can have less of an impact on population growth rate than in less stressful abiotic conditions. A subadditive effect of herbivory in more stressful abiotic conditions can further be explained by a decrease in the contribution of early life stage transitions and increase in the contribution of later life stage transitions to population growth rate. Furthermore, our results suggest low wet season precipitation can decrease *S. obovata* population growth rate more than mollusc herbivory (Figure 3.2).

The results of this research have several applied restoration implications. First, our research illustrates that for short-lived species like *S. obovata*, a decrease in inter-annual precipitation can have a greater negative effect on population dynamics than seedling herbivory. Secondly, as abiotic conditions become more stressful the removal of non-native herbivores may have less of an effect on reversing population decline and extinction. Furthermore, our results suggest that assisted migration (i.e., introduction of species into new environments) may be necessary for rare plant populations to persist in geographical areas that are projected to decrease in wet-season precipitation over time.

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Table 3. 1 Location of a single population of *Schiedea obovata* in the Kahanahaiki Management Unit, in the northern Waianae Mountain Range on the island of Oahu.

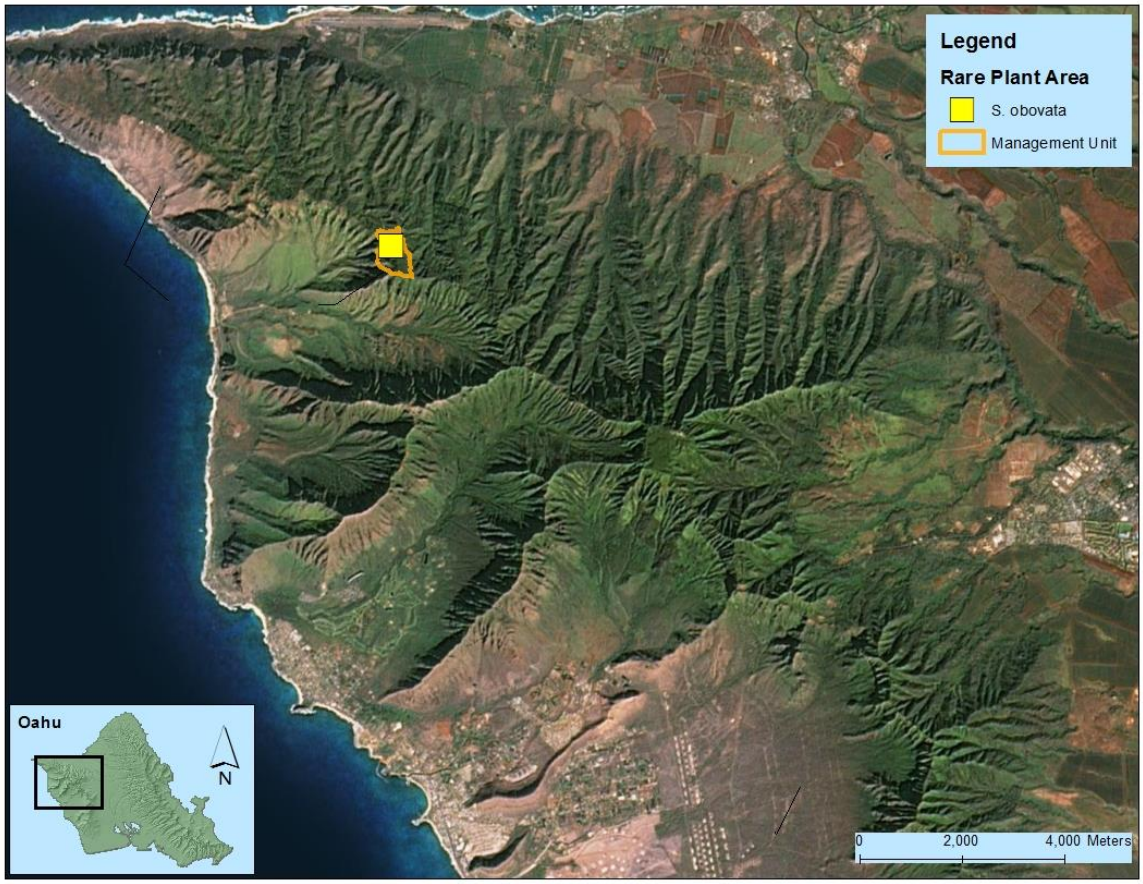

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Table 3. 2 Generalized linear mixed-effect models of survival $s(x, a)$, growth $g(x, a)$, probability of fruiting $\boldsymbol{f_f(x,a)}$, and reproductive output $\boldsymbol{p_r(a)}$. The models in grey represent the most complex model with a Δ AICc < 2. Size = height to apical meristem, number of seedlings = number of seedling at time t per mature plant at t+1, and precipitation represents total wet season precipitation. For all models, plot and plant ID were included as random effects.

Estimate *t* Δ AICc							
		Intercept	Size	Precipitation	Size X Precipitaiton	df	Δ AICc
Survival	size	1.49	0.65	-	-	4	6.9
	size + precipitation	1.67	0.65	-0.02	-	5	7.5
	size X precipitation	-0.77	0.06	-0.16	0.12	6	0.0
Growth	size	1.49	0.65	-	-	5	0.0
	size + precipitation	1.67	0.65	-0.02	-	6	6.5
	size X precipitation	1.95	0.54	-0.06	0.02	7	13.9
Probability of fruiting	size	-10.29	2.78	-	-	4	7.7
	size + precipitation	-13.90	3.15	0.28	-	5	0.0
	size X precipitation	-9.27	1.82	-0.31	0.17	6	1.0
Reproductive output	size	-1.47	0.41	-	-	5	14.8
	precipitation	-0.42	-	0.07	-	5	0.0
	size + precipitation	-4.68	0.87	0.15	-	6	11.2
	size X precipitation	4.77	-1.64	-0.93	0.29	7	4.7

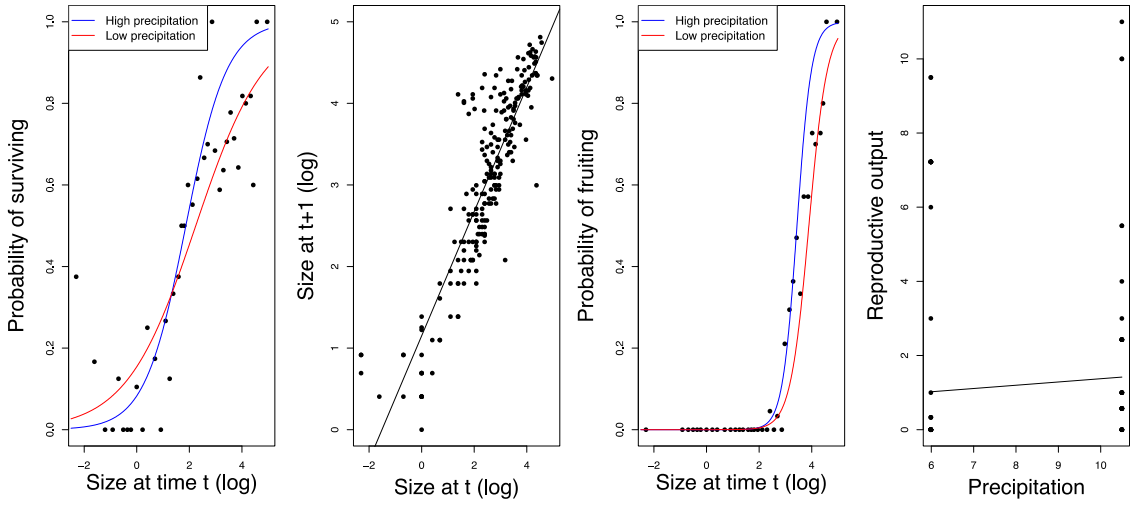

Figure 3. 1 Regression models of survival $s(x, a)$, growth $g(x, a)$, probability of fruiting $\boldsymbol{f_f(x, a)}$, and reproductive output $\boldsymbol{p_r(a)}$. The solid blue line represents high precipitation and the solid red line represents low precipitation.

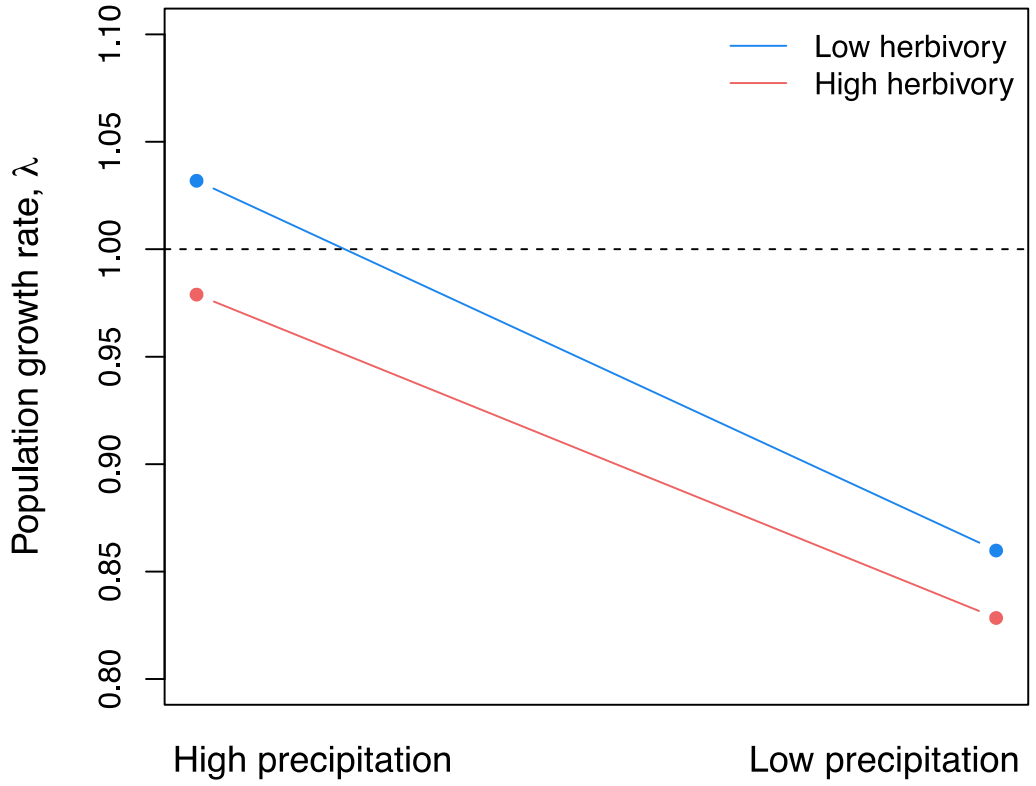

Figure 3. 2 The asymptotic population growth rate λ for scenarios: i) high wet season precipitation and low herbivory (HP-LH), ii) high wet season precipitation and high herbivory (HP-HH), iii) low wet season precipitation and low herbivory (LP-LH), and iv) low wet season precipitation and high herbivory (LP-HH).

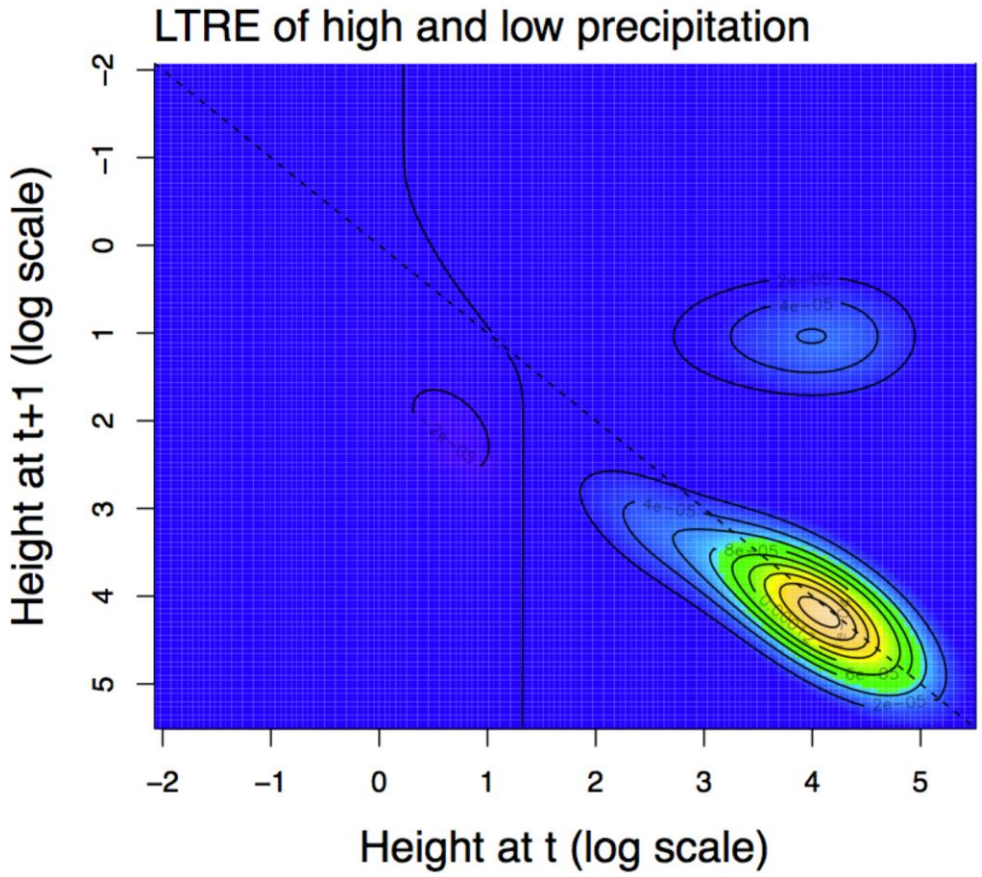

Figure 3. 3 Life table response experiment (LTRE) of *Schiedea obovata,* which decomposes the variation in the population growth rate λ of low wet season precipitation, relative to high wet season precipitation. The dashed line represents survival of *S. obovata*. Area to the left of the solid line has a negative effect on λ and area to the right of the solid line has a positive effect on λ.

Chapter 4 Evaluating both the transient and asymptotic dynamics is critical for assessing the efficacy of species reintroductions

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Abstract

1: The reintroduction of species into natural preserves and the suppression of top-down stressors are commonly used restoration strategies to prevent the extinction of critically endangered species. These strategies create new populations that are dominated by a single stage class (e.g., large plants used for outplanting), which can cause the population dynamics to fluctuate in the near-term before it reaches a stable equilibrium. Gaining an understanding of how the dynamics of reintroduced population will fluctuate in the near-term transient phase is critical for developing effective restoration strategies.

2: In this five-year study, we assessed the near-term transient (i.e., 10 year projections) and asymptotic long-term population dynamics of a multi-years reintroduction effort of a critically endangered long-lived shrub, *Delissea waianaeensis*. Additionally, we quantified the effect of temporal variability in seedling recruitment on the transient and asymptotic population growth rates.

3: We found that the near-term transient and the asymptotic long-term population growth rates differed. When the probability of high recruitment years is 17%, mimicking the observed field conditions, the population is projected to grow in the near-term but decline in the long-term. In order for the population to persist over time required an increase in the probability of high seedling recruitment years to $\geq$ 50%. The survival of mature plants was the most important vital rate for the long-term growth of the population, whereas seedling recruitment was the most important to the near-term dynamics when the high recruitment years was $\geq$ 50%.

4: *Synthesis and application*. This research illustrates that when plant reintroductions are established with large vegetative and reproductively mature plants, the population will grow faster in the transient phase than in the long-term (i.e., transient amplification) as the stage structure approaches equilibrium. We suggest that management of additional threats that influence recruitment should be considered for this plant species. Our results are relevant to other long-lived species reintroductions that are established with later life stages, and illustrate how important it is evaluate both the transient short-term and asymptotic long-term dynamics to fully understand the likely outcome of species reintroduction efforts.

Introduction

Population reintroduction and the suppression of exotic competitors and predators are commonly used strategies to prevent the extinction of rare species (Soorae, 2013, Maschinski and Haskins, 2012). The end goals of this management strategy are to establish new populations that will persist in the long-term and promote species recovery (Falk et al., 1996, Pavlik, 1996). With an increase in rare and at-risk species (IUCN, 2013) and continued anthropogenic change in environmental conditions, population reintroduction has become an integral component of many recovery efforts (Maunder, 1992). While many studies have evaluated the initial success of rare species reintroductions by quantifying various measures of fitness, such as the survival of reintroduced individuals and rates of natural regeneration (Godefroid et al., 2011, Menges, 2008), few studies have investigated how likely and under what conditions reintroduced populations will persist over time (but see, Bell et al., 2003, Maschinski and Duquesnel, 2007, Liu et al., 2004, Colas et al., 2008, Bell, 2013). The limited number of studies that have examined the dynamics of rare species reintroductions is due, in part, to the lack of comprehensive long-term demographic data that quantifies vital rates of reintroduced and naturally recruited individuals in these new populations. Demographic studies that have evaluated the likely outcome or rare species reintroduction efforts have primarily used the long-term asymptotic dynamics as a response metric and yielded mixed results (Colas et al., 2008, Bell et al., 2003, Maschinski and Duquesnel, 2007). For some species, reintroduced populations were projected to persist in the long-term (Bell et al., 2003, Maschinski and Duquesnel, 2007). In other scenarios, the long-term asymptotic

growth rates were <1, indicating the populations would decline over time (Colas et al., 2008, Bell et al., 2003).

To establish reintroduced populations it is a common practice to use large immature individuals (Bell et al., 2003, Maschinski and Duquesnel, 2007), a mix of seeds and small immature plants (Bell et al., 2003), and seeds (Colas et al., 2008). However, given reintroduced populations are often started with a cohort of a single life stage (e.g., only seeds or only reproductively mature individuals) and such new populations are likely far from their stable equilibrium, it is expected that the near-term transient and long-term population dynamics will diverge (Haridas and Tuljapurkar, 2007, Koons et al., 2005, Fox and Gurevitch, 2000). In the near-term transient phase, the population growth rate depends on temporal shifts in plant vital rates and the resulting change in population structure (Haridas and Tuljapurkar, 2007). In extreme cases, year-to-year fluctuations in vital rates and the resulting population structure can cause extinction prior to the population reaching equilibrium (Fox and Gurevitch, 2000). Therefore, understanding the transient and long-term dynamics of reintroduced populations can aid decision making about management actions that need to be taken to ensure both short and long-term success of reintroduction efforts. There is a growing body of literature that has examined the transient dynamics of natural populations following the removal of environmental stressors that altered the stage structure of the populations, including herbivory pressure (Maron et al., 2010), harvesting (Gaoue, 2016), and habitat disturbance (Ezard et al., 2010b, Bialic‐Murphy et al., 2017). However, the near term

transient phase of newly established populations is rarely examined (but see, Ezard et al., 2010b, Wong and Ticktin, 2015).

The Hawaiian Islands are a biodiversity hotspot, with an estimate of over 89% of the flowering plant species being endemic (Wagner et al., 1999). In Hawaii, over 40% of endemic species are listed as critically endangered or threatened (USFWS, 2012), 99% of which are threatened by multiple anthropogenic stressors (Wilcove et al., 1998) including habitat conversion and rapid invasion of non-native competitors, predators, and pathogens (Cuddihy and Stone, 1993, Wilcove et al., 1998). Though non-native species are the primary drivers of species endangerment globally, their effects are thought to be more severe for island species. The greater effect of non-native species on islands is due in part to the absence of mammalian predators (and other herbivore and predator functional groups). Given many herbivores and predators were historically absent throughout there range, island plants often have low mechanistic and physiologic tolerance to these consumers (Gillespie & Clague 2009; Whittaker & Fernández-Palacios 2007).

Across oceanic islands, such as Hawaii, rare species reintroduction and suppression of top-down stressors has become a critical component of restoration efforts (Maschinski and Haskins, 2012). Some stressors can be removed with little long-term management follow-up. For example, an initial investment in a fence to exclude non-native ungulates can provide long-term removal of this top-down stressor with little ongoing maintenance costs. However, a reduction in the abundance of other biotic

stressors, such as invasive competitors, invertebrate predators (e.g., slugs), and small vertebrate predators (e.g., rodents) requires long-term and ongoing maintenance (e.g., annual removal of invasive competitors, frequent trapping of rodents) (Maschinski and Haskins, 2012). A pressing question for conservation is whether the removal of the most ubiquitous environmental stressors (e.g., non-native ungulates) and the reintroduction of endangered species are enough to create viable populations, or if other, more difficult to manage, stressors also need to be mitigated.

In this study, we assessed the population dynamics of a multi-year population reintroduction effort of a Hawai‘i endemic shrub, *Delissea waianaeensis* Lammers (Campanulaceae). This reintroduced population has been actively managed for over two decades, including the suppression of feral pigs (*Sus scrofa*) and non-native ecosystem altering vegetation. At the start of the study, in 2010, the reintroduced population was composed of outplanted mature individuals and first filial plants in all life stages. The objectives of this study were to: (1) quantify how the dynamics of the *D. waianaeensis* reintroduction will change over time as the stage structure approaches a stable equilibrium, (2) identify what part of the life cycle, if improved by management, would have the greatest positive impact on the transient and asymptotic population dynamics, and (3) investigate the influence of temporal variability in seedling recruitment on the transient and asymptotic dynamics.

Materials and methods

Study species

Delissea waianaeensis (Campanulaceae) is a critically endangered tree endemic to the island of O'ahu. The Campanulaceae group is the largest Hawaiian angiosperm family (Givnish et al., 2009) and is also one of the most threatened Hawaiian groups, with over 25% of the endemic Hawaiian species extinct (USFWS, 2012). *Delissea waianaeensis* has a single or branched erect stem and is 1–3 meters tall at first reproduction (Wagner et al., 1999). It produces fleshy purple, red, white, and pink berries, which is indicative of frugivorous bird dispersal (Lammers, 2005). The floral sugar composition suggest *D. waianaeensis* was historically pollinated by native birds in the honeycreeper (Drepanidinae) and Hawaiian Mohoideae (Mohoidae) groups (Lammers and Freeman, 1986, Pender, 2013). Following massive extinction of native birds in the Drepanidinae and Mohoidae groups, it is likely that *D. waianaeensis* is dispersal and pollen limited (Lammers and Freeman, 1986, Pender, 2013). *Delissea waianaeensis* is found between 245–760 m elevation, along the north facing slopes and gulch bottoms of the Waianae Mountain Range (Wagner et al., 1999). In 1996, *D. waianaeensis* was listed as federally endangered (USFWS, 1998) and by 2005 it was restricted to seven geographically isolated locations (USFWS, 2012).

Study site and reintroduction details

The study site is in the Central Kaluaa gulch of the Honouliuli Forest Reserve, which is located in the northern Wai‘anae Mountains, on the island of O‘ahu (HON; 21° 28’ N, -158°6’ W). The mean monthly rainfall is 52–171 mm (Giambelluca et al., 2013). The site represents a tropical mesic forest, composed of mixed native and non-native flora and fauna (OANRP, 2011). Selection of the reintroduction site was based on

similarities of associated species and relatively accessible location in the historic geographical distribution of naturally occurring *D. waianaeensis* (Dan Sailer, personnal communication). In 2001, The Nature Conservancy constructed the Central Kaluaa fence, eradicated feral pigs, and implemented invasive vegetation control for the protection of *D. waianaeensis* and other managed taxa.

In 2002, The Nature Conservancy initiated reintroduction of *D. waianaeensis* into the Central Kaluaa Gulch, starting with the clearing of invasive species across the reintroduction location and the outplanting of 43 mature plants. The founders used for the Kaluaa *D. waianaeensis* reintroduction were from a relictual geographically isolated population of five individuals, located 4,000 m from the outplanting site. Stock from the other six geographically isolated populations was not used for the Kaluaa reintroduction to avoid potential outbreeding depression and the loss of local adaptations (Kawelo et al., 2012). Prior to outplanting, seeds from the five Kaluaa founders were grown in a greenhouse for one growing season. In 2004, the management of the Kaluaa *D. waianaeensis* reintroduction was transferred to the O‘ahu Army Natural Resources Program (OANRP) and incorporated into a larger conservation plan to offset the potential impact of military training operations on 89 rare species. OANRP outplanted an additional 303 plants from 2004–2012. The 2012 outplanting included genetic representation from two additional individuals that were discovered in close proximity to the five original founders used for the Kaluaa reintroduction. The mean plant height at the time of outplanting was 56 cm.

Data collection

From 2010–2015, we collected annual demographic data for a total of 597 permanently tagged plants at the field site. The life cycle of *D. waianaeensis* was categorized into four life stages: reproductively mature (>35 cm and reproductive), large immature (> 35 cm and vegetative), small immature (2 cm – 35 cm), and seedling (< 2 cm). The population stage structure at the start of the study included 74 reproductively mature plants, 131 small and large immature plants, and 217 seedlings. Each year of the study a minimum of 50 plants in the reproductively mature, large immature, and small immature life stages were permanently tagged and vital rate data were collected. All individual seedlings in the population were permanently tagged and vital rate data was collected annually from January to February. For each tagged plant the survival, height to the apical meristem, and fertility (i.e. fruit production) were recorded.

Data analysis

Projection matrix construction

We used the demographic data to construct a Lefkovitch matrix **A** (Caswell, 2001) for each transition year 2010–2011, 2011–2012, 2012–2013, 2013–2014, and 2014–2015. The 4 x 4 matrix **A** can be decomposed into two matrices: a survival-growth matrix **U** and fertility matrix **F**. Matrix **A** captured the yearly transition probability of survival σ, the probability of growing to the next stage class γ, and seedling recruitment φ_m in the following discrete life stages: reproductively mature (*m*), large immature *(li*), small immature (*si)*, and seedling (*s)*. The term φ_m represents the mean number of seedling produced per mature plant. For the φ_m term, we were able to calculate an additional transition year 2009–2010.

$$\mathbf{A} = \begin{pmatrix} \sigma_s(1-\gamma_s) & 0 & 0 & \varphi_m \\ \sigma_s\gamma_s & \sigma_{si}(1-\gamma_{si}) & 0 & 0 \\ 0 & \sigma_{si}\gamma_{si} & \sigma_{li}(1-\gamma_{li}) & 0 \\ 0 & 0 & \sigma_{li}\gamma_{li} & \sigma_m \end{pmatrix}$$

The dominant eigenvalue of matrix **A** represents the long-term population growth rate λ, with an associated stable stage distribution *w* and reproductive value *v* (Caswell, 2001).

Temporal variability of seedling recruitment φ_m

To model the effect of temporal variability of recruitment as a stochastic process, we first created an array for seedling recruitment that consisted of φ_m values for transition years 2009–2010, 2010–2011, 2011–2012, 2012–2013, 2013–2014, and 2014–2015, which are referred to hereafter as years **1–6**. We then classified seedling recruitment φ_{m1-6} in years **1–6** as either *high* (*h*) and *low* (*l*). Seedling recruitment φ_{m1} in year 1 was 3.09 seedlings per mature individual and seedling recruitment φ_{m2-6} in years 2–6 ranged from 0.569 to 0.021 seedlings per mature individual. We classified seedling recruitment φ_{m1} in year 1 as *high* and seedling recruitment φ_{m2-6} in years 2–6 as *low*. To evaluate the influence of temporal variability in seedling recruitment φ_m on population dynamics we created an array of **F** matrices for a total of six scenarios **F1**–**F6**, which are described below, by modifying the probability of high and low recruitment being selected following a temporally stochastic process. Independent of the fertility matrices **F**, we used our survival-growth data 2010–2011, 2011–2012, 2012–2013, 2013–2014, and 2014–2015 to create an array of **U** matrices.

Stochastic asymptotic population dynamics

To project the near-term transient and long-term asymptotic dynamics, we used a stochastic stage-structured model (Caswell, 2001):

$$n(t+1) = \mathbf{X}(t)n(t) \quad (1)$$

where $\mathbf{X}(t)$ is equal to the sum of selected **U** and **F** matrices, one from a pool of five **U** matrices (2010–2011, 2011–2012, 2012–2013, 2013–2014, and 2014–2015) and the other from a pool of six **F** matrices (2009–2010, 2010–2011, 2011–2012, 2012–2013, 2013–2014, and 2014–2015) at a given time *t*. The vector $n(t)$ is the number of individuals in each stage class at a given time t, and $n(t+1)$ is the total number of individuals at time $t+1$. We used this framework to project population dynamics for six scenarios **F1**– **F6**, differing in temporal variability of recruitment. For scenario **F1** the probability of a high seedling recruitment years (h) being selected each time step t was 16.66%. Scenario **F1** mimicked the probability of high seedling recruitment years based on observed field conditions (i.e., 1 in 6 years). For scenarios **F2**– **F6,** we increased the probability that a high seedling recruitment year (h) was selected each time step t in order to simulate an increase in high recruitment by one year for each consecutive scenario. Scenarios **F2**– **F6** ranged from a 33% to a 100% probability of a high seedling recruitment year (h) being selected each time step t (i.e., 2 in 6 years). For all scenarios **F1**– **F6,** matrix **U** was selected with equal probability at each time step t from the pool of **U** matrices.

For scenarios **F1**– **F6,** we calculated the stochastic long-term growth rate λ_s by simulation, using 50,000 iterations following Tuljapurkar *et al* (2003):

$$\log\lambda_s = \lim_{t\to\infty}\left(\frac{1}{t}\right)\log[\mathrm{N}(t)/\mathrm{N}(0)], \quad (2)$$

where $\mathrm{N}(t)$ is the population size at time t, which is the sum of *n*(t) at a given time t. For

each scenario, 95% bootstrap confidence intervals were calculated following methods outlined in Morris and Doak (2002). In addition to projecting the asymptotic stochastic population growth rate for scenarios **F1**– **F6**, we conducted stochastic elasticity analysis to identify the relative importance of perturbations in vital rates on the stochastic population growth rate λ_s with respect to perturbation of the mean and variance E^s (Tuljapurkar et al., 2003, Haridas and Gerber, 2010).

This reintroduced population of *D. waianaeensis* was initiated with all large-sized individuals, and thus the population structure was initially far from its stable stage distribution. To project the stochastic transient population growth rate r_s for scenarios **F1**–**F6**, we simulated 10,000 independent sample paths of t = 10 years. For each scenario **F1**–**F6**, we altered the probability of a high (h) seedling recruitment year using the method described above. To mimic a plant reintroduction that is established using only reproductively mature individuals, we set the initial stage structure $n(0)$ to 100% reproductively mature individuals and 0 for the other life stages. Using a cohort of later life stages (e.g. reproductively mature individuals) is particularly relevant from an applied management perspective because reintroduced population are often established with later life stages since these individuals have the highest rate of initial establishment (Maschinski and Haskins, 2012). To identify the relative importance of life stages on the stochastic transient population growth rate for scenarios **F1**–**F6** we conducted stochastic transient elasticity analysis e^s, which is composed of the instantaneous influence of a one time step change in vital rates e_{ij}^1 and the long-term influence of perturbations in the stage structure e_{ij}^2 (Haridas and Gerber, 2010, Haridas and Tuljapurkar, 2007).

Results

The long-term stochastic population growth rate λ_s for scenario **F1,** which represents the field recruitment rate (16.66% probability of high recruitment years)**,** was 0.967 (95% CI of 0.963 to 0.972), indicating that the population will decline by 3.3% per year (Figure 4.1b). A two-fold increase in the probability of high recruitment years from 17% to 33% (scenario **F2**) resulted in a stable population growth rate (λ_s =0.996 [0.995, 1.00]). A three-fold increase in the probability of high recruitment years from 17% (scenario **F1**) to 50% (scenario **F3**) shifted the long-term stochastic population dynamics from a 3.3% decline to a 2% increase in the population size per year ([λ_s =1.020, [1.015, 1.026]; Figure 4.1b). Similarly, the long-term stochastic population growth rates λ_s were > 1 for scenarios **F4**–**F6** (Figure 4.1b). Conversely, the reintroduced population of *D. waianaeensis* was projected to grow moderately in the near-term transient phase for all scenarios (Figure 4.1a).

The survival of mature plants (stasis) was projected to have the greatest impact on the long-term stochastic population growth rate for all scenarios **F1**–**F6** (Figure 4.2b). Increasing high recruitment years positively influenced the relative importance of the transition from seedling to small immature for the long-term population growth rate. However, this did not change the ranking of which life stage transition had the greatest effect on the population growth rate (Figure 4.2b). Similar to our results for the long-term stochastic elasticity analysis, survival of mature plants (stasis) had the greatest impact on the near-term population growth rate for scenarios **F1**–**F2** (Figure 4.2a). Interestingly, when the probability of high seedling recruitment years was ≥ 50% (i.e., scenarios **F3–**

F6) seedling recruitment had a greater influence than mature plant survival on the near-term dynamics (Figure 4.2b).

Discussion

Few studies have used a demographic modeling approach to assess the likely outcome of rare species reintroductions (but see, Colas et al., 2008, Bell et al., 2003, Maschinski and Duquesnel, 2007), and all of these have focused on the long-term asymptotic dynamics. However, to fully understand the likely outcome of rare species reintroductions it is critical to assess how these populations will fluctuate in the near-term transient phase prior to reaching a stable equilibrium. Previous studies that have examined the transient dynamics of newly established population have yielded mixed results. Plant populations of a culturally important non-timber forest product, *Alyxia stellata*, which was restored by outplanting immature individuals, were projected to decline faster in the transient phase than over time (Wong and Ticktin, 2015). Similarly, newly established populations of invasive species following seed dispersal were found to grow slower early in the invasion process than over time as later life stages filled in and the stages structure approaches equilibrium (Ezard et al., 2010b). Conversely, following the exclusion of herbivores, which negatively affected fertility and earlier life stages, plant populations were projected to grow faster in the near term than in the long-term (Maron et al., 2010, Bialic‐Murphy et al., 2017). In this study, we used five years of demographic data to compare the short and long-term dynamics of a multi-year reintroduction effort of a critically endangered long-lived shrub, *Delissea waianaeensis.*

For *D. waianaeensis*, we found that the population was projected to grow moderately over the next 10 years (Figure 4.1a). Conversely, the population was projected to slowly decline in the long-term (Figure 4.1b). This more optimistic short-term projection of plant dynamics is explained by the newly established population, which was dominated by large outplanted individuals. The higher growth rate in the transient phase than in the asymptotic phase can be explained by the high initial reproductive value of the population, which can cause population amplification prior to reaching a stable stage equilibrium (Stott et al., 2011). Since large individuals are more likely to survive and successfully establish a new population, conservation biologists typically use these individuals for reintroduction projects (Maschinski and Haskins, 2012). For these reintroductions, our results suggest that short-term estimates of success should be interpreted with caution since transient dynamics will likely be more positive than long-term dynamics. This result is generalizable to other perennial plant reintroductions that are established with large outplanted individuals. Our results also demonstrate that the control of targeted environmental stressors and population reintroduction can lead to an increase in the short-term population growth rate but may not always be enough to establish new populations that will persist over time.

Previous studies have demonstrated that perturbations of earlier life stages are often more important in the transient phase than in the asymptotic phase (Bialic‐Murphy et al., 2017, Haridas and Gerber, 2010, McMahon and Metcalf, 2008, Miller and Tenhumberg, 2010, Fox and Gurevitch, 2000). It has also been shown that anthropogenic stressors can have a greater negative effect on the short-term population growth rate

under more optimal abiotic conditions than less optimal abiotic conditions (Gaoue, 2016). Consistent with previous studies, we found that the short and long-term population growth rates and the elasticity patterns for *D. waianaeensis* diverge and varied based on the probability of years with high recruitment. We also found that in order for *D. waianaeensis* to persist over time would require doubling the probability of a high recruitment year from 17% (i.e., the observed field conditions) to 50% (Figure 4.1b). Additionally, we found that perturbation of the survival of reproductively mature *D. waianaeensis* was projected to have the greatest relative influence on the stochastic population growth rate (Figure 4.2b). Similarly, changes in the survival of mature plants were projected to have the greatest relative influence on the transient population growth for scenarios **F1**– **F2**. However, when the probability of high recruitment years was ≥ 50% (i.e., scenarios **F3**– **F6)**, perturbation of seedling recruitment, not mature plant survival, was projected to have the greatest influence on the transient population growth rate. These results are consistent with previous research, which illustrate that key vital rates, including survival and fertility, that contribute to asymptotic population growth also have a strong influence of transient dynamics (Stott et al., 2010). Thus, populations that grow faster in the long-term asymptotic phase are more likely to experience greater magnitudes of transient amplification (Stott et al., 2010). Combined, our results and previous studies illustrate that the relative importance of vital rates on the near term population growth rate is dependent, in part, on the level of habitat disturbance and variability of key life processes.

Environmental stochasticity can increase the risk of extinction (Tuljapurkar et al., 2003) and cause the short and long-term population to diverge (Stott et al., 2010). For *D. waianaeensis,* we found that seedling recruitment was temporally variable, with high seedling recruitment in 2009–2010 and low recruitment from 2010–2015 (ranging from 0.02–0.57) (see Appendix S1). Considering the many sources of environmental stochasticity (e.g., changing abiotic conditions, boom-and-bust cycles of seedling herbivores), this variability in seedling recruitment was not surprising. However, our results emphasize the need to understand the mechanisms responsible for this variability in seedling recruitment, as this vital rate has a strong influence on the likely outcome of restoration efforts. As mentioned previously, we found that an increase in the probability of a high recruitment year from 17% to 50% would be required for the population to persist over time (Figure 4.1b). However, it should be noted that we did not account for potential autocorrelation of stochastic processes, which can strongly influence the dynamics of structured populations (Tuljapurkar and Haridas, 2006, Gaoue et al., 2011) and should be a focus of future research.

Implementing conservation recommendations stemming from stochastic perturbation analysis can be challenging (Ehrlén and Groenendael, 1998, Mills et al., 1999). Though perspective elasticity analysis is often used to indicate which demographic processes needs to be modified by management to maintain endangered species that will persist over time, these recommendations may not be feasible in a naturally variable environment and conservation biologists must adapt their strategy (Ehrlén and Groenendael, 1998, Mills et al., 1999). In this study, we found that for scenarios that

were projected to persist over time (scenarios **F3**– **F6**), management efforts aimed at increasing seedling recruitment were the most beneficial to the population when they occur early in the reintroduction process (i.e., while the population is experiencing transient dynamics) (Figure 4.2a). Conversely, for scenarios that were projected to decline over time (scenarios **F1**– **F2**), maintain high survival of mature plants in the transient phase was projected to be more important (Figure 4.2a). However, with relatively high *D. waianaeensis* mature plant survival there is little that can be done by management to improve this vital rate. Conversely, there are several potential management options to increase seedling recruitment, including suppression of invasive frugivores and herbivores.

Two of the primary invasive species that negatively influence recruitment of oceanic island species are black ship rat (*Rattus rattus*) and leopard slug (*Limax maximus*) (Joe and Daehler, 2007, Shiels et al., 2014). Over the 2015 fruiting season, we found that black ship rats consumed 85% of *D. waianaeensis* mature fruits at the study site (Lalasia Bialic-Murphy, unpublished data). Furthermore, the leopard slug is a known non-native seedling herbivore in Hawai‘i and has been documented at the study site (Kawelo et al., 2012, Joe and Daehler, 2007). In Hawaii natural areas, the density of black ship rats (Shiels, 2010) and leopard slugs (Stephanie Joe, personal communication) fluctuate from year-to-year. Thus, it is likely that the variable intensity of frugivory by black ship rats and seedling herbivory by leopard slugs are underpinning mechanisms driving temporal fluctuations in seedling recruitment. Considering the observed boom-and-bust cycles of black ship rats and leopard slugs, it is also likely that the probability of

years with high *D. waianaeensis* recruitment would likely increase if conservation biologists prioritize the suppression of top-down stressors in years with high frugivory and herbivory pressure. Previous studies suggest that management actions that reduce boom-and-bust cycles of environmental stressors, such as non-native pests, can reduce the risk of extinction (Tuljapurkar et al., 2003) However, to fully understand the effects of black ship rats and leopard slugs on targeted vital rates and plant dynamics further investigation is needed.

This research has several applied restoration implications. First, our results illustrate that when later life stages are used to establish plant reintroductions, the population will grow faster in the transient phase than in the asymptotic phase as the stage structure reaches equilibrium (i.e., transient amplification) (Stott et al., 2011). Secondly, the effect of management action (e.g., increasing the survival of seedling or mature individuals) on the population growth rate depends on the timescale of interest and is context specific. Globally, this study illustrates that the removal of the most ubiquitous top-down stressors (e.g., non-native pigs) and population augmentation will not always be enough for species in degraded ecosystems to persist over time (i.e., long-term stochastic growth rate $\lambda > 1$). For these species, the suppression of other top down stressors needs to be considered. Furthermore, the results of this research emphasize how critical it is to evaluate both the near-term transient and long-term dynamics of endangered species in order to fully understand the likely outcome of species reintroduction efforts and develop effective restoration strategies.

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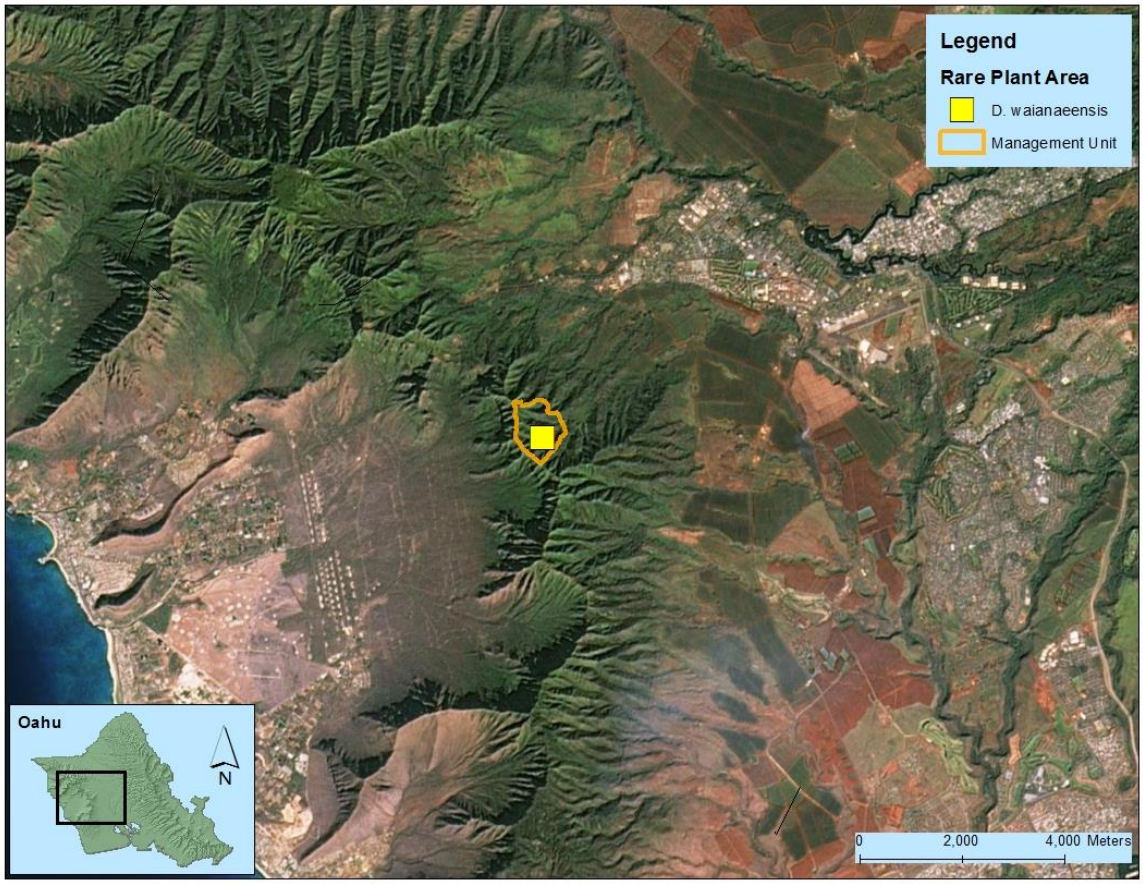
Table 4. 1 Location of a single population of *Delissea waianaeensis* in the Kaluaa Management Unit, in the Waianae Mountain Range on the island of Oahu.



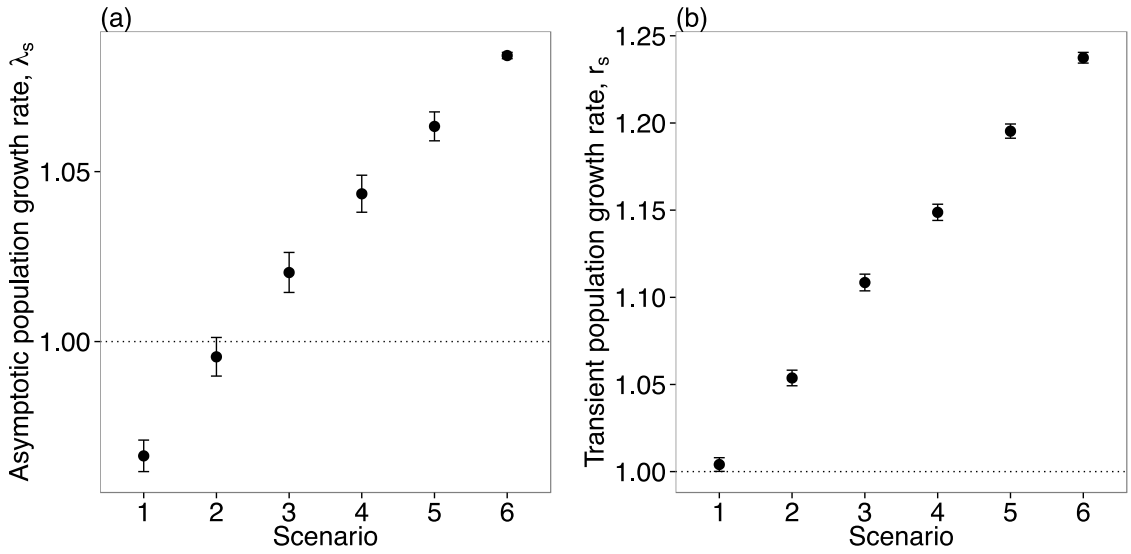


Figure 4. 1 Asymptotic and transient growth rates with 95% confidence intervals, calculated from 1000 bootstrap samples. For scenario 1 (i.e., field conditions), the probability of high recruitment years was 17% (i.e., every six years). For scenario 2–6, the probability of high recruitment increased by one year for each consecutive simulation.

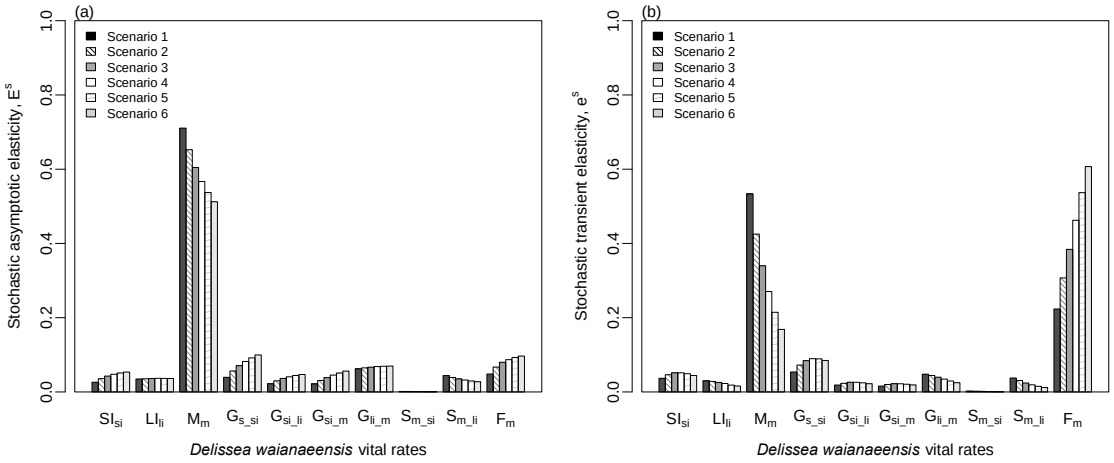


Figure 4. 2 Asymptotic and transient elasticity. Seedling (S); small immature > 40cm (SI); large immature, >40cm (LI); and mature signs of reproduction (M). For scenario 1 (i.e., field conditions), the probability of high recruitment years was 17% (i.e., every six years). For scenarios 2–6, the probability of high recruitment increased by one year for each consecutive simulation.

Chapter 5 Using Transfer Function Analysis to develop biologically and economically efficient reintroduction strategies for endangered species

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Running title: Economically and biologically efficient management

Keywords: transfer function analysis, marginal relative efficiency, population reintroduction, population dynamics, restoration ecology, and elasticity analysis.

Abstract

1: One of the most widely used strategies to prevent species decline is to suppress top-down stressors. For species with few remaining individuals, reintroduction is also used to prevent imminent extinction. Following the reintroduction, it is often challenging to identify what level of threat control is needed for species to persist over time. Threat control and the reintroduction of endangered species are time intensive and costly. Thus, it is critically important to develop economically efficient restoration strategies.

2: In this study, we combined transfer function analysis and economic cost analysis to evaluate the effect of biologically meaningful increases in demographic processes on the persistence of a reintroduced population of an Hawaii endemic long-lived shrub, *Delissea waianaeensis* (Campanulaceae), following the suppression of a non-native frugivorous rodent (*Rattus rattus*) and invasive molluscs.

3: We show that a 41% increase in fertility following the suppression of rodents or an 8% increase in seedling growth following the suppression of molluscs would stabilize the *D. waianaeensis* population (i.e., $\lambda = 1$). Though a greater increase in fertility than seedling growth was needed for the reintroduced population to persist over time, increasing fertility by suppressing rodents was the most cost effective restoration strategy.

4: *Synthesis and application.* Globally, our study emphasizes how important it is to incorporate the economic cost of management actions in demographic models when developing restoration plans for endangered species. Establishing biologically and

economically efficient restoration strategies are particularly needed for species reintroductions.

Introduction

For extremely rare species, population reintroduction and the suppression of threats are commonly used restoration strategies to prevent imminent extinction (Maschinski and Haskins, 2012). The ultimate goal of these restoration strategies are to achieve long-term population persistence and promote the recovery of species over time (Maschinski and Haskins, 2012). However, a recent review suggests that the long-term persistence of reintroduced populations is alarmingly low (Drayton and Primack, 2012). The low rate of persistence of reintroduced populations is likely due to the widespread disturbance of ecosystems in which rare species occur and the adverse effects of invasive species. In these altered landscapes, it is essential to identify which threats need to be suppressed, following species reintroduction, to achieve the desired outcome (i.e., population growth rate $\lambda \geq 1$). With limited funding for conservation and the high costs of population reintroduction and the suppression of threats, it is also critically important to identify the most economically efficient restoration strategy.

Demographic population models combined with elasticity analysis are common tools that can identify which vital rate, if improved by management, would have the greatest positive effect on the population growth rate of endangered species (Miller et al., 2011, De Kroon et al., 2000). This analytical approach is a linear approximation of the relative importance of plant vital rates on population dynamics, and is therefore an appropriate tool for assessing the effect of small changes in vital rates on population growth rate. Previous studies, however, demonstrate that the relative importance of plant vital rates on population dynamics is dependent, in part, on the magnitude of the

perturbation and this relationship is often nonlinear (Dahlgren et al., 2011, De Kroon et al., 2000, Knight et al., 2009). Thus, elasticity analysis may lead to suboptimal conclusions when prioritizing conservation actions that can have large effects on targeted vital rates. Unlike elasticity analysis, transfer function analysis accounts for the nonlinear relationship between vital rates and population growth rates and is a more appropriate approach to evaluate the influence of targeted changes in vital rates on the population growth rate at the magnitude of interest (Stott et al., 2012a, Hodgson et al., 2006, Hodgson and Townley, 2004). An additional benefit of transfer function analysis is its capability of simultaneous perturbations of multiple vital rates (Hodgson and Townley, 2004). For these reasons, transfer function analysis is particularly useful for evaluating conservation strategies for species threatened by multiple environmental factors.

When there are multiple combinations of management actions that would likely result in the desired outcome, it is also important to identify which restoration strategy is the most cost effective. Some management actions require high upfront fixed costs (e.g., equipment costs) but low continual ongoing maintenance (e.g., labor) and other management actions require low upfront costs but high continual ongoing maintenance. Thus, it is not always intuitive which strategy will be the most cost effective in the long-term. Though rarely used, demographic modeling provides an ideal framework to explicitly compare the economic cost of various management actions when developing restoration strategies (but see, Baxter et al., 2006).

In chapter 4, we evaluated the viability of a reintroduced population of the endangered Hawaiian shrub, *Delissea waianaeensis* Lammers (Campanulaceae) that is threatened by multiple factors, including non-native ungulates, plants, rats and molluscs. Removal of non-native ungulates and invasive plant management is not enough for this species to persist over time. In the present study, we used demographic models and transfer function analysis to identify which additional environmental stressors need to be suppressed to achieve population persistence and develop economically efficient restoration strategies. Specifically, our objectives were to (1) assess the effect of changes in seedling growth and fertility on the population growth rate of *D. waianaeensis* across a range of biologically meaningful perturbations, (2) identify the percent increase in targeted vital rates that would be enough for the population to persist following the reduction in abundance of *R. rattus* and non-native molluscs, and (3) quantify the economic cost and efficiency to suppress *R. rattus* and non-native molluscs.

Material and methods

Study species

Delissea waianaeensis is a single or branched O‘ahu endemic shrub typically reaching 1–3 m in height (Wagner et al., 1999). The fleshy fruit is an ovoid berry with purple, red, white, to pink exocarp and white mesocarp (OANRP, unpublished data). The size of *D. waianaeensis* seeds are between 1.0–1.2 mm long and 0.4–0.6 mm wide (WagnerHerbst et al., 2005). Seed viability of *D. waianaeensis* is relatively high, with a 95% mean germination rate (OANRP, 2016). The fleshy fruit produced by *D. waianaeensis* is indicative of frugivorous bird dispersal (Pender, 2013). The floral sugar

composition suggests *D. waianaeensis* was historically pollinated by native birds in the honeycreeper (Drepanidinae) and Hawaiian Mohoideae (Mohoidae) groups (Lammers and Freeman, 1986, Pender, 2013, Lammers, 2005). Following massive extinction of birds in these groups, it is likely that *D. waianaeensis* is dispersal and pollen limited (Lammers and Freeman, 1986, Pender, 2013).

Rattus rattus (black ship rat) is one of the most disruptive vertebrates to invade oceanic islands and often listed as a primary driver of species decline and extinction (Towns et al., 2006, Shiels et al., 2014). The estimated home range of *R. rattus* is 4 ha (Shiels, 2010).When foraging, *R. rattus* are the most active in areas with thick understory vegetation cover 10–30 cm in height (Shiels, 2010). *Rattus rattus* dens are often below ground in soil and fractured rock substrate, under logs, in thick understory vegetation, and inside partially dead trees (Shiels, 2010). Thought *R. rattus* are omnivores, seeds and fruits are the dominant portion of their diet (Shiels et al., 2014). Following consumption and digestion by *R. rattus*, small seeds (0.5–1.2 mm) remain intact and viable (Shiels and Drake, 2011). The relatively small size of *D. waianaeensis* seeds (1.0–1.2 mm) suggests that *R. rattus* do not alter seed viability of this taxon following consumption and digestion. However, the large home range, den characteristics, and foraging behavior of *R. rattus* imply *D. waianaeensis* seeds consumed by *R. rattus* are deposited in unsuitable habitat for seedling establishment.

The establishment of non-native molluscs (Mollusca: Gastropoda) is often implicated in the decline of oceanic island species (Cowie et al., 2009, Joe and Daehler,

2007). Molluscs are generalist herbivores, primarily consuming foliage on the forest floor. In Hawaii, a total of 12 different non-native mollusc species have established throughout natural areas (Cowie, 1999, Cowie, 1997). In mesic to wet forest communities in Hawaii, terrestrial molluscs significantly reduce the density of numerous native seedlings and thus, the suppression of non-native molluscs is often incorporated as part of the recovery strategy for endangered species (Kawelo et al., 2012, Joe and Daehler, 2007).

Study site and reintroduction details

The study site is in the Central Kaluaa gulch of the Honouliuli Forest Reserve, which is located in the northern Waiʻanae Mountains, on the island of Oʻahu (HON; 21° 28' N, -158°6' W). The mean monthly rainfall is 52–171 mm (Giambelluca et al., 2013). The Central Kaluaa gulch is a tropical mesic forest with a mix of native and non-native flora and fauna (OANRP, 2011). The *D. waianaeensis* population is a multi-year reintroduction effort that is composed of both outplanted individuals and naturally established plants in all life stages. The *D. waianaeensis* population has been actively managed for over a decade, first by the Nature Conservancy and then the Oʻahu Army Natural Resources Program (OANRP). Over a ten-year timeframe, from 2002–2012, a total of 346 individual plants were outplanted at the Central Kaluaa reintroduction site. In 2001, feral ungulates were removed from the Honouliuli Forest Reserve. At the *D. waianaeensis* study site, there is also ongoing suppression of invasive vegetation (for additional details of the restoration see Chapter 4).

Data collection

The life cycle of *D. waianaeensis* was categorized into four life stages: reproductively mature individuals (>35 cm and capable of reproduction), large immature (> 35 cm and non-reproductive), small immature (2 cm–35 cm), and seedling (< 2 cm). From 2010–2015, a total of 597 individuals plants were permanently tagged and demographic data were collected annually in January–February. For each tagged plant we recorded survival, growth to the apical meristem, and reproduction (i.e., vegetative, flowering, or fruiting).

Using the demographic data from 2010–2015, we constructed a mean 4x4 Lefkovitch **A** matrix. The mean **A** matrix captures the probability of survival σ, the probability of growing to the next stage class γ, and seedling recruitment φ_m in the following discrete life stages: reproductively mature (*m*), large immature *(li*), small immature (*si*), and seedling (*s*). The term φ_m is the mean total number of seedling produced at time $t+1$ by the total number of reproductively mature plants at time t. Since we had an additional year of data for fertility, the φ_m term of matrix **A** is the mean fertility over six consecutive years from 2009–2015. Matrix **A** is used to calculate the population growth rate (i.e., dominant eigenvalue λ) and the elasticity of λ to perturbations in matrix elements (Caswell, 2001).

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & \varphi_m \\ \sigma_s\gamma_s & \sigma_{si}(1-\gamma_{si}) & 0 & 0 \\ 0 & \sigma_{si}\gamma_{si} & \sigma_{li}(1-\gamma_{li}) & 0 \\ 0 & 0 & \sigma_{li}\gamma_{li} & \sigma_m \end{pmatrix}$$

Data analysis

Transfer function analysis

The exact relationship between the magnitude of change (δ) in targeted vital rates and the population growth rate (i.e., dominant eigenvalue λ) is as follows (Stott et al., 2012b):

$$\delta^{-1} = \mathbf{c}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\,\mathbf{d} \qquad \text{eqn 1}$$

where matrix **A** represents the transition matrix and **I** is the identity matrix with the same dimensions of matrix **A.** The terms **c** and **d** represent row and column vectors that determine the vital rates that will be perturbed. The term δ denotes the magnitude of the perturbation. We used eqn 1 to quantify the response in population growth rate λ to a range of biologically meaningful perturbations δ (Davis et al., 2006), using the popdemo package in R version 3.1.0 (Stott et al. 2012b). We specifically tested the response to biologically meaningful (a) increases in fertility φ_m following the suppression of *R. rattus*, and (b) increases in seedling growth γ_s following the suppression of non-native molluscs. We also identified the magnitude of perturbation δ for fertility φ_m and seedling growth γ_s that would be needed to reach a stable population growth rate (i.e, λ_{pert} = 1(Stott et al., 2012b).

The range of biologically meaningful perturbations that we used for this study was determined using a combination of field experiments and the results of previous studies. To set a realistic range of increases in fertility φ_m following the suppression of *R. rattus*, we quantified the percent of fruits consumed and the identity of the consumer using a modified version of the methods developed by Pender et al. (2013). Specifically,

we installed 24 tracking tunnels at equal distance along four transects (50 cm x 10 cm x 10 cm; Connovation Limited, Auckland, New Zealand), with tracking cards inserted (The Black Trakka Gotcha Traps LTD, Warkworth, New Zealand) (Figure 5.1). The four transects spanned the length of the *D. waianaeensis* population; capturing intrapopulation habitat heterogeneity. Each tracking tunnel was baiting with one mature fruit and checked at a two-day interval. On each visit, fruit consumption was recorded and the tracking tunnels were re-baited. The footprints left on the tracking cards each visit were used to identify the frugivore consuming *D. waianaeensis* fruits (Figure 5.1). In total, the tracking tunnels were baited five times during the 2015 fruiting season. In this field experiment, we found that the mean number of *D. waianaeensis* fruits consumed by *R. rattus* was 83%. To mimic the impact of *R. rattus* on fertility and population dynamics, we used the mean number of *D. waianaeensis* fruits consumed at our field site to set the range of biologically feasible increases in φ_m (i.e., 1%–83%) that could be achieved by suppressing *R. rattus*. The proportion of fruits consumed by *R. rattus* at the *D. waianaeensis* population was consistent with previous studies that have examined the effect of *R. rattus* on the fertility of a related taxon in the Campanulaceae group, *Cyanea superba* ssp. *superba* (Pender et al., 2013).

To set a range of biologically meaningful increases in seedling growth γ_s following the suppression of non-native molluscs, we used the results of a previous field experiment (Kawelo et al., 2012). In this experiment, 200 seeds of three localized Hawaiian endemic species (*Cyanea superba* ssp. *superba, Cyrtandra dentata, and Schiedea obovata*) were sown on the top layer of soil in 12 plots, 15m x 15m in diameter.

Six plots were treated with a molluscicide, Sluggo (Neudorff Co., Fresno, California), and the other six plots were left exposed to normal herbivory intensity at the field site. The density of seedlings in each plot was recorded on a weekly basis for six weeks. This study illustrated that non-native molluscs significantly reduced seedling density of localized endemic plants by up to 33% (Kawelo et al., 2012). The range of biologically feasible increases in γ_s following the suppression of non-native molluscs that we used in our study was 1%–33%.

Relative marginal efficiency

To calculate the marginal efficiency to suppress non-native molluscs and *R. rattus* we used the following equation (Baxter et al., 2006):

$$\epsilon_k = \frac{\partial \lambda}{\partial c_k} \qquad \text{eqn 2}$$

where $\partial C_k$is the change in cost for achieving a management action k (i.e., increase in targeted vital rate) and $\partial \lambda$ represents the change in the population growth rate following the investment in management k. The change in population growth rate $\partial \lambda$ following the investment in k was calculated using eqn 1. The efficiency of two management actions, *n* and *m*, can be estimated by calculating the relative marginal efficiency $x = \epsilon_n/\epsilon_m$. If the relative marginal efficiency x is >1, then management action *n* is more efficient than *m*.

The costs to suppress *R. rattus* C_f and molluscs C_s were derived from the OANRP database and represent the average cost to suppress *R. rattus* and molluscs at other managed sites of comparable size to the *D. waianaeensis* site. The suppression of *R. rattus* and molluscs both require an investment in variable costs (e.g., wages). The suppression of *R. rattus* also requires an upfront investment in fixed costs (e.g.,

equipment). To incorporate the cost of equipment needed to suppress *R. rattus* on a yearly basis, the fixed costs (e.g., equipment) were amortized over the lifespan of the equipment (Lewis and Pendrill, 2004). The total cost to suppress *R. rattus* C_f was calculated as the sum of the fixed and variable annual costs.

To suppress *R. rattus* at the *D. waianaeensis* field site would require 20 Goodnature A24 self-resetting multi-species kill traps (Tyler Bogardus, personal communication). The per unit cost of the Goodnature A24 self-resetting multi-species kill trap was $125 and the lifespan of the traps was 10–15 years (Tyler Bogardus, personal communication). The total field time needed to setup the *R. rattus* trap grid and maintain it over one *D. waianaeensis* fruiting season was 60 hours ($25.92 per hour x 60 hours = $1,555.2; Oahu Army Natural Resources Program, unpublished data). The total yearly field time needed to suppress molluscs was 176 hours ($25.92 per hour x 176 hours = $4,562; Oahu Army Natural Resources Program, unpublished data). The lower total field time needed to suppress *R. rattus* than to suppress molluscs is due, in part, to the shorter duration of time that *R. rattus* needs to be suppresses. While *R. rattus* only needs to be suppressed during the *D. waianaeensis* fruiting season, molluscs need to be suppressed year round. The fixed cost of equipment to suppress *R. rattus* was $2,500 (i.e., 20 Goodnature A24 rodent traps x $125 per trap). However, when amortized over the lifetime of the equipment (i.e., 10 years), the yearly equipment cost to suppress *R. rattus* was $250. Including labor costs, the total yearly cost to suppress *R. rattus* (i.e., yearly fixed cost of equipment and labor costs) was $1,805. For mollusc suppression, there is no upfront fixed cost of equipment and the total yearly labor cost was $4,562.

Results

The effects of vital rate perturbations on the population growth rate of *D. waianaeensis* were nonlinear across a range of biologically meaningful perturbations (Figure 5.2). Specifically, the change in population growth rate decreased as the perturbation of fertility, growth of seedlings, and shrinkage of mature plants increased (Figures 5.2). Conversely, the percent change in population growth rate increased as the perturbation magnitude in the stasis of all life stages and the growth of small vegetative plants increased (Figure 5.2). Assuming a linear relationship of the relative importance of plant vital rates on population dynamics, our results indicate that perturbations in the survival of mature plants would have the greatest effect on population dynamics (Figure 5.3). However, survival of mature plants is already high (86%), and this is not a vital rate that can be improved with management (Figure 5.4). The two vital rates that can be improved by management, fertility and seedling growth, have the same elasticity value (Figure 5.3). However, a substantially larger increase in fertility (41%) than seedling growth (8%) was required to shift the population growth rate from declining to stable (i.e., $\lambda = 1$, Figure 5.5). There were also multiple combinations of increases in seedling growth and increases in fertility that achieved this desired outcome (Figure 5.5). Furthermore, the increases in either fertility or seedling growth that improved the population growth rate were within the range of biologically feasible perturbations (Figures 5.2 and 5.5).

The increases in fertility (71%) following the suppression of *R. rattus* and increase in seedling growth following the suppression molluscs (33%) that were used to calculate the marginal efficiency of each management action were based on the results of

previous field experiments for related species (Kawelo et al., 2012, Pender et al., 2013). Using transfer function analysis, we found that these perturbation values translated to an increase in population growth rate from 0.97 to 1.01 and from 0.97 to 1.05, respectively. The relative marginal efficiency x of increasing fertility ϵ_f and seedling growth ϵ_s on population growth rate was 1.20 (*i.e.*, $x = \epsilon_f/\epsilon_s$), which indicates the suppression of *R. rattus* is more economically efficient than the suppression of molluscs.

Discussion

The long-term persistence of reintroduced populations is alarmingly low (Stott et al., 2012a, Hodgson and Townley, 2004). Thus, more threat management is necessary post-reintroduction to ensure the long-term persistence of most reintroduced species. In this context, it is critical that conservation biologists identify cost-effective combinations of restoration actions. Managing rare plant species native to oceanic islands is particularly challenging, as these species are typically threatened by numerous factors, some of which are more difficult to manage than others (Kawelo et al., 2012). In this study, we identified the demographic processes that need to be improved by management post-reintroduction to ensure the long-term persistence of a long-lived shrub in Hawaii. Furthermore, we quantified which combination of threat control actions, including the suppression of *R. rattus* and molluscs, would be the most cost efficient.

Large perturbations in fertility and earlier life stages can have smaller effects on population growth rate than would be expected based on elasticity analysis, which considers small perturbations in vital rates (Hodgson and Townley, 2004). Ignoring the biological limits in targeted vital rates when prioritizing restoration actions can also lead

to ineffective management recommendations (Lubben et al., 2008). For example, Lubben et al. (2008) found that management recommendations based solely on elasticity analysis, which ignores biological limits, would indicate conservation biologists should focus on increasing the survival of adult Serengeti cheetah. However, when the magnitude of change in targeted vital rates were considered they found that multiple vital rates needed to be increased in order for Serengeti cheetah to persist, including the survival of adult and newborn cubs. Consistent with previous studies, our results demonstrate that changes in fertility and seedling growth on population growth rate decreased as the magnitude of change in these parameters increased (Hodgson and Townley, 2004). Supporting previous findings (Lubben et al., 2008), our study also illustrates the need to consider biological limits to fully understand what part of the life cycle, if improved by management, would have the greatest effect on population dynamics. Specifically, management recommendations based on elasticity analysis showed equal preference for management that improves fertility and management that improves seedling growth. However, using transfer function analysis, which account for non-linear population dynamics response (Hodgson and Townley, 2004), we found that a greater increase in fertility (41%) than seedling growth (8%) was needed in order for *D. waianaeensis* to persist over time (Figure 5.5). Thus, considering only the magnitude of change in fertility and seedling growth that would be needed to reach the desired outcome for *D. waianaeensis* (i.e., cost negligent model), our results would suggest management should focus on improving seedling growth.

There is a growing literature that demonstrates seed consumption by rodents is an important threat to many rare plant species, especially in systems for which the rodents are introduced (Shiels et al., 2014, Traveset et al., 2009, Auld et al., 2010), or occur at unnaturally high densities due to human modification of landscapes (Dangremond et al., 2010, Pardini et al., 2017). Similarly, seedling herbivory by molluscs is known to be significant threats for native plants to oceanic islands, especially Campanulaceae species such as *D. waianaeensis* (Cowie et al., 2009, Joe and Daehler, 2007, Shiels et al., 2014, Towns et al., 2006, Kawelo et al., 2012). In this study, we found that the increases in demographic vital rates expected from threat control of either molluscs or *R. rattus* would shift the population growth rate from declining to stable or growing (i.e., $\lambda \geq 1$). Surprisingly, when the costs of threat control management were explicitly included in our demographic model (i.e., cost efficient model) there was a shift in management recommendations from prioritizing the suppression of molluscs to prioritizing the suppression of *R. rattus*. There are several reasons for the higher economic efficiency of *R. rattus* control than mollusc control. First, there are large differences in management-induced changes in targeted vital rate follow threat control. While fertility can increase by up to 83% following the suppression of *R rattus*, seedling growth can only increase by up to 33% following the suppression of molluscs (Kawelo et al., 2012). Secondly, it is less expensive to suppress rodents than it is to suppress molluscs. The lower cost of rodent suppression than mollusc suppression is due, in part, to the shorter duration of time that rodents need to be suppressed. While rodents only need to be suppressed during the *D. waianaeensis* fruiting season, molluscs need to be suppressed year round. Furthermore, technological advancements, such as the development of the self-resetting Goodnature

A24 rodent traps, have improved the efficiency and reduced the labor hours needed to suppress rodents (Franklin, 2013). Similar advancements in the technological advancement of mollusc control have not been achieved and should be a focus of future applied research and policy considerations. Further, we note that additional research is needed for *D. waianaeensis* to explicitly measure the realized effects of managing both rodents and molluscs, since the response in vital rates used for our economic models were based on field experiments for related species (Kawelo et al., 2012, Pender et al., 2013).

There is a broad body of literature that has examined the effects of invasive pests on the demography of rare plant and animal species (Crone et al., 2011). Surprisingly, to our knowledge, only one study has directly linked the economic cost of targeted threat control actions to changes in the population growth rate of managed species (Baxter et al., 2006). This study found that incorporating costs of targeted restoration explicitly in demographic models resulted in optimal management recommendations that diverged from the cost-negligent managed recommendations. Specifically, elasticity analysis would focus on increasing the survival of the endangered Australian Helmeted Honeyeater, whereas cost-efficient management recommends would focus on increasing fecundity by reducing nest predation (Baxter et al. 2006). Consistent with this study, we found contrasting management recommendations based on the results of our cost-efficient and cost-negligent demographic models. Management recommendations based on the results of cost-negligent model would suggest conservation biologists should focus on increasing seedling growth by suppressing molluscs. Conversely, we found that improving fertility by reducing fruit consumption by *R. rattus* would be more cost

effective and should therefore be prioritized. The time is ripe for more demographic analyses that explicitly incorporate the cost of various management actions for conservation planning. Many rare plant and animal populations have detailed demographic data and face multiple threats. Typically, approximate estimates for the economic costs of management are also readily available.

Future research that incorporates varying levels of threat control intensity would greatly improve our understanding of restoration optimization that accounts of economics of scale. Due to the rarity of *D. waianaeensis,* we were limited to one site for this study. Thus, our results are not generalizable across a range of ecological conditions or varying levels of threat control intensity. Regardless, this study provides an example of how to develop efficient and effective management strategies for declining populations. Specifically, this study demonstrates the usefulness of transfer function analysis to set biologically meaningful increases in targeted vital rates that would be needed to reach a predefined restoration goal (e.g., population growth rate $\lambda \geq 1$). Further, when multiple management strategies could be used to reach the desired restoration outcome, our results illustrate how important it is to incorporate the cost of targeted threat control actions in demographic models in order to optimize management efficiency. Considering the limited financial resources allocated to conservation and the continual increase in the listing of rare and at-risk species (IUCN, 2013), using demographic models to identify the most economically efficient restoration strategy is becoming increasing important.

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Figure 5. 1 The image to the left is a photo of the tracking tunnels (50 cm x 10 cm x 10 cm; Connovation Limited, Auckland, New Zealand) used to quantify fruit consumption by *Rattus rattus*. The image to the right is a tracking card (The Black Trakka Gotcha Traps LTD, Warkworth, New Zealand) with footprints of *Rattus rattus* following fruit consumption.

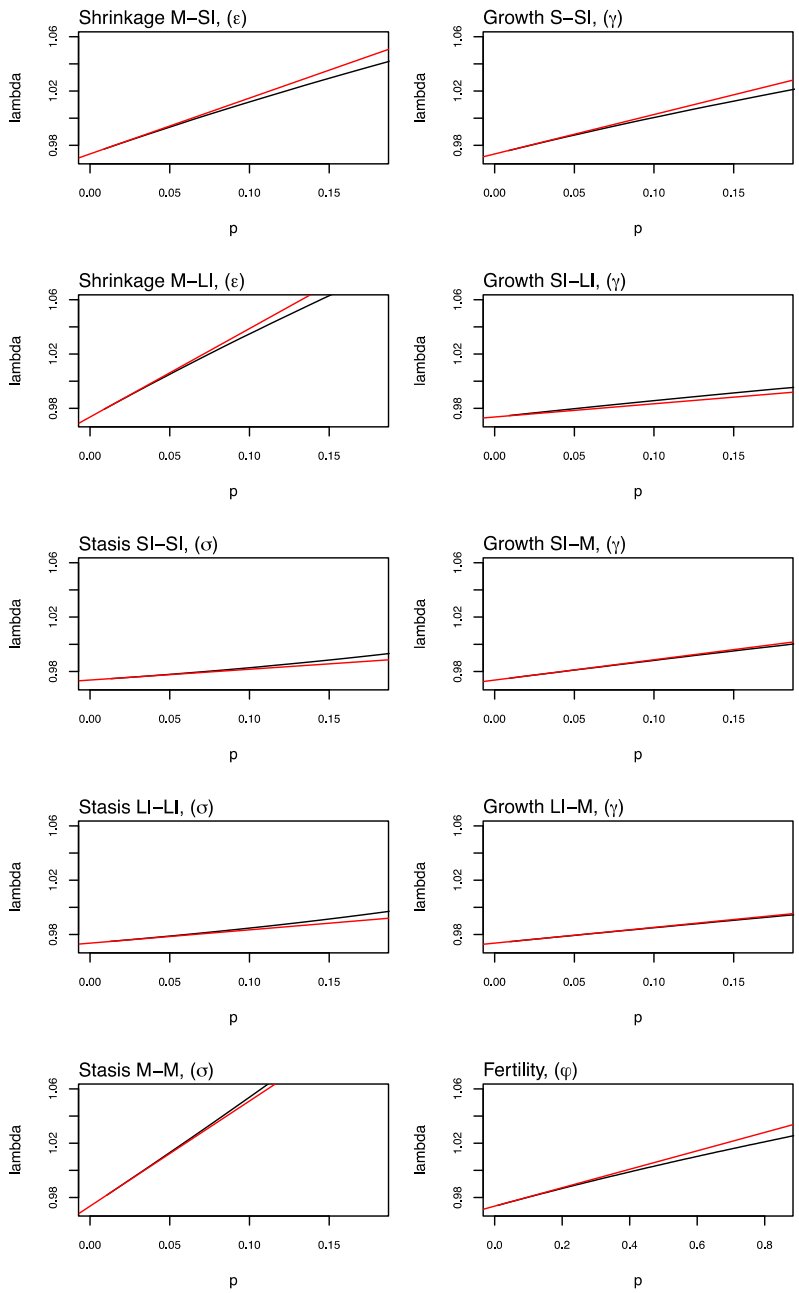

Figure 5. 2 Transfer function analysis, where the black line illustrates the change in population growth rate across a range of biologically meaningful perturbations in the vital rates and the red line represents the slope for the sensitivity of vital rates. The vital rates are fertility ($\boldsymbol{\varphi}$), survival ($\boldsymbol{\sigma}$), growth ($\boldsymbol{\gamma}$), and shrinkage ($\boldsymbol{\varepsilon}$) and the life stages are seedling (S), small immature (SI), large immature (LI), and mature (M).

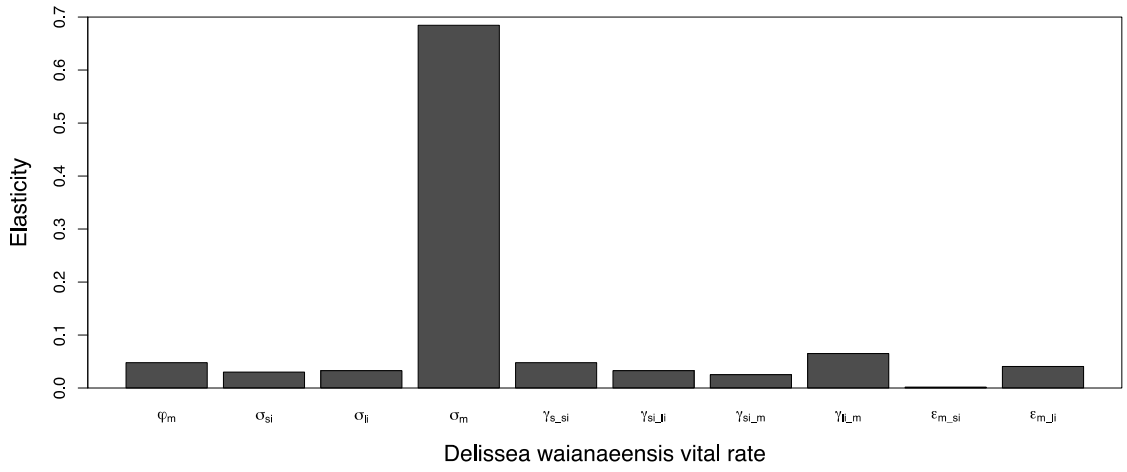

Figure 5. 3 Elasticity analysis, which illustrates the change in population growth rate to small perturbations in vital rates. The vital rates are fertility ($\boldsymbol{\varphi}$), survival ($\boldsymbol{\sigma}$), growth ($\boldsymbol{\gamma}$), and shrinkage ($\boldsymbol{\varepsilon}$). The life stages are life stages are seedling (S); small immature > 40cm (SI); large immature, >40cm (LI), and mature signs of reproduction (M).

	S	SI	LI	M
S	0.000	0.000	0.000	0.687
SI	0.161	0.368	0.000	0.004
LI	0.000	0.188	0.326	0.061
M	0.000	0.163	0.544	0.860

Figure 5. 4 Mean yearly transition matrix for of *Delissea waianaeensis.* The life stages are life stages are seedling (S); small immature > 40cm (SI); large immature, >40cm (LI), and mature signs of reproduction (M).

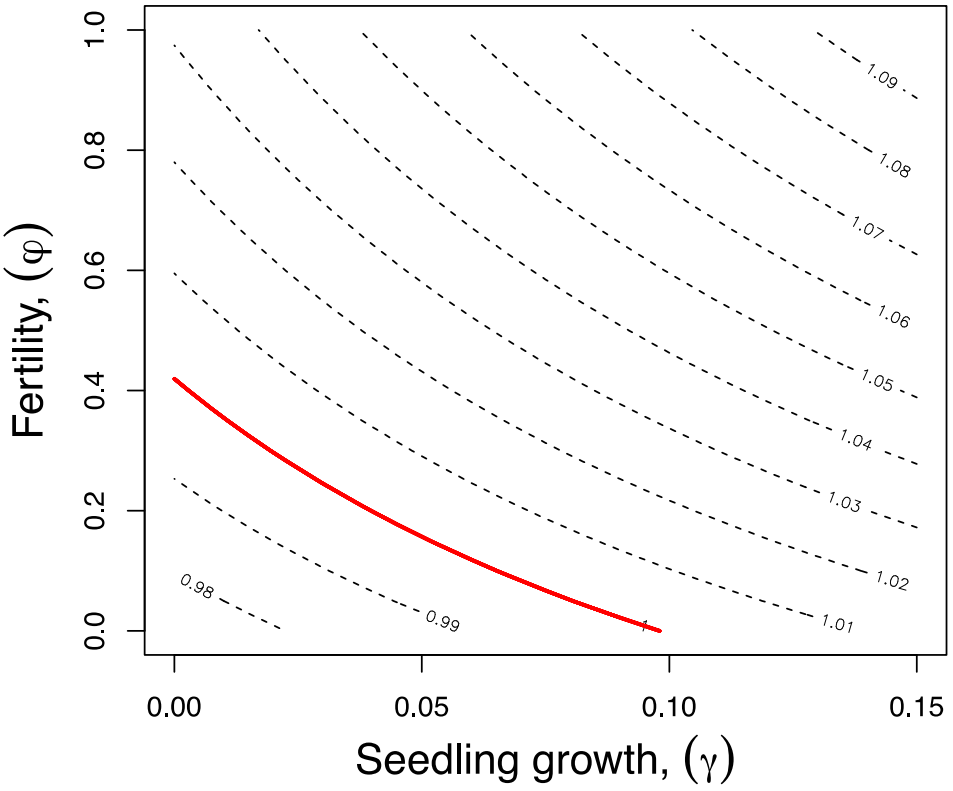

Figure 5. 5 Exact perturbation analysis, which represents the combined effect of perturbations in fertility and seedling growth on the population growth rate of *Delissea waianaeensis* across a range of biologically meaningful values.

Chapter 6 Conclusions

The primary aim of this dissertation was to examine the effects of environmental change on the population dynamics of localized endemic species confined to narrow ecological conditions. Specifically, I used a combination of size and stage structured demographic models to compare how abiotic parameters and dominant non-native pests influence key demographic processes and ultimately plant fitness. Additionally, I examined the near term transient and long-term asymptotic dynamics of critically endangered plants to gain insight into the likely outcome of commonly used restoration strategies, including the suppression of non-native pests and population reintroduction.

In Chapter 2, I used four years of demographic data to develop matrix projection models for a long-lived shrub, *Cyrtandra dentata* St. John & Storey (Gesneriaceae). Furthermore, I evaluated the individual and combined influence of a non-native frugivorous bird, *Leiothrix lutea*, and microhabitat heterogeneity on the short-term and long-term *C. dentata* population dynamics. Frugivory by *L. lutea* decreased the short-term and long-term population growth rates. However, under the current level of frugivory at the field site the *C. dentata* population was projected to persist over time. Conversely, the removal of optimum microhabitat for seedling establishment (i.e., rocky gulch walls and boulders in the gulch bottom) reduced the short-term and long-term population growth rates from growing to declining. In this study, I also found that the survival of mature *C. dentata* plants had the greatest influence on long-term population dynamics, followed by the growth of seedlings and immature plants. The importance of mature plant survival was even greater when I simulated the combined effect of frugivory

and the loss of optimal microhabitat, relative to population dynamics based on field conditions. In the short-term (10 years), however, earlier life stages had the greatest influence on population growth rate. The results of this chapter emphasize how important it is to decouple rare plant management strategies in the short versus long-term in order to prioritize restoration actions, particularly when faced with multiple stressors not all of which can be feasibly managed. From an applied conservation perspective, my findings also illustrate that the life stage that, if improved by management, would have the greatest influence on population dynamics is dependent on the timeframe of interest and initial conditions of the population.

In the Chapter 3, I used a size dependent integral projection model (IPM) to evaluate how inter-annual precipitation and molluscan herbivory influenced the temporal variability in the dynamics of a Hawaiian endemic short-lived herb, *Schiedea obovata* (Caryophyllaceae). My results suggest wet season precipitation had a greater effect on population growth rate of *S. obovata* than mollusc herbivory and the impact of precipitation on plant vital rates shifted across plant ontogeny. Furthermore, wet season precipitation influenced multiple vital rates in contrasting ways and the effect of precipitation on the survival of larger vegetative and reproductively mature individuals contributed the most to variation in the population growth rate λ. I also found a synergistic effect of precipitation and herbivory, with a greater negative effect of herbivory on population growth rate λ in years with high wet season precipitation. On a broad scale, this chapter highlights the importance of evaluating how abiotic factors and plant-consumer interactions influence an organism across its life cycle to fully understand

the underpinning mechanisms that structure its spatial and temporal distribution and abundance. The results of this chapter also illustrate that the effect of plant-herbivore interactions on plant population dynamics is context specific and for short-lived species, like *S. obovata*, seedling herbivores can have less of an effect on the dynamics of plant populations than abiotic conditions.

To investigate the population dynamics of plant reintroduction efforts, in Chapter 4 I assessed the near term transient (i.e., 10 year projections) and asymptotic (long-term) dynamics of a multi-year reintroduction of a critically endangered long-lived shrub, *Delissea waianaeensis* (Campanulaceae). I also quantified the impact of temporal variability in seedling recruitment on transient and asymptotic population growth rates. In the short-term, the reintroduced population of *D. waianaeensis* was projected to grow moderately. However, in the long-term the population was projected to slowly decline. To shift the long-term population growth rate from declining to growing required an increase in frequency of high recruitment years from 17% (i.e., the observed field conditions) to 50%. Furthermore, the relative importance of mature plant survival had the greatest effect on the long-term population growth rate. Conversely, the relative importance of mature plant survival on the short-term growth rate decreased as the frequency of high seedling recruitment years increased. When the frequency of high seedling recruitment years was > 50%, the life stage that was projected to have the greatest effect on the transient population growth rate shifted from mature plant survival to seedling recruitment. This study demonstrates that plant reintroductions established with later life stages will grow faster in the short-term than in the long-term (i.e., transient

amplification), as the stage structure approaches equilibrium. Globally, this chapter illustrates that short-term estimates of reintroduction success should be interpreted with caution. This is particularly true when later life stages are used to establish populations since transient dynamics will be more positive than long-term dynamics.

Lastly, in Chapter 5 I evaluated the effect of biologically meaningful increases (i.e., perturbations) in survival, growth, and fertility on the dynamics of declining population of *D. waianaeensis.* I also assessed the percent increase in fertility and seedling growth that would be needed for *D. waianaeensis* to persist following the suppression of invasive molluscs and a non-native frugivorous rodent, *Rattus rattus*. Additionally, I quantified the relative marginal efficiency to suppress molluscs and *R. rattus.* My results suggest a greater increase in fertility (41%) than seedling growth (8%) would be needed to shift the population growth rate from declining to persistent over time (i.e., $\lambda = 1$). Based on the results of a cost negligent demographic model, I found that non-native molluscs would be the optimal restoration strategy. However, when the economic cost of each threat control action was explicitly incorporated in the model the suppression of *R. rattus* was more economically efficient than the suppression of molluscs and thus, an optimal strategy. Globally, this chapter illustrates how critical it is to evaluate the effect of biologically meaningful changes in vital rates on population dynamics when prioritizing restoration actions. Furthermore, this study emphasizes how important it is to quantify the economic cost of targeted threat control actions when developing management strategies.

Challenges and Future Direction

Studying the demography of rare and endangered species is challenging due to limited replication (Morris and Doak, 2002). Despite the constraint of limited replication valuable insight can be gained from studying the population dynamics of endangered species, such as quantifying the likely outcome of management actions and assessing the potential impact of environment parameters on population dynamics (Dostálek and Münzbergová, 2013, Ellis et al., 2007, García, 2003, Marrero-Gómez et al., 2007, Crone et al., 2011, Morris et al., 2002). Detailed population-level demographic studies can also be used to identify the underpinning demographic processes driving variation in plant dynamics and be a proactive method of predicting the likely outcome of management actions, which would otherwise take several generations to detect (Menges, 2000). For this study, I was limited in replication due to species rarity and obtaining permission to access field sites. Thus, results from this study may not be extrapolated across varying habitat and ecological parameters. Future integrative studies on the combined impact of plant interactions with multiple environmental parameters would benefit from having replication across multiple study sites. Furthermore, the population level responses of endangered plants to environmental change should be studied for more species varying in life history in order to evaluate if generalized patterns emerge, which could be used to effectively manage rare plants and the habitat that they depend on. Further investigation is also needed to compare the ecological and economical costs of various restoration actions in order to develop efficient and effective management strategies. This is particularly true for endangered species that occur in extremely altered landscape with numerous environmental stressors, not all of which can be feasibly managed. In this

context, it is critical to identify which combination of management actions will not only reach the desired outcome but are also the most economically efficient.

Regardless of the difficulties of studying endangered species, the results of this study illustrate how important it is to decouple the impacts of environmental change on the dynamics of endangered species in order to fully understand the drivers of species decline and extinction. From an applied conservation perspective, our findings also illustrate that the life stage that, if improved by management, would have the greatest influence on population dynamics is dependent on the timeframe of interest and initial conditions of the population. Furthermore, this research suggests that the asymptotic long-term dynamics are not always an accurate proxy of plant dynamics over the short-term (i.e., transient phase). Decoupling the differences in the near term transient dynamics and long-term asymptotic dynamics may be particularly important for improving the success of species reintroduction efforts. Additionally, this research emphasizes how important it is to decouple rare plant management strategies in the short versus long-term in order to develop efficient and effective management strategies. The results of this dissertation also illustrate that the effect of plant-animal interactions on plant population dynamics can be context specific and for species, like *S. obovata* and *C. dentata*, non-native pests can have less of an effect on plant dynamics than degradation in microhabitat quality and decreased inter-annual precipitation.

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